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Benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies

Olivier Beauchard^{1,2,*}, Sebastiaan Mestdagh¹, Leo Koop³, Tom Ysebaert^{1,4}, Peter Herman⁵

¹Netherlands Institute for Sea Research and Utrecht University, Department of Estuarine and Delta Systems, Korringaweg 7, PO Box 140, Yerseke 4401 NT, The Netherlands

²University of Antwerp, Ecosystem Management Research Group, Universiteitsplein 1, 2610 Wilrijk, Belgium

³Delft University of Technology, Acoustics Group, Delft 2629 HS, The Netherlands

⁴Wageningen Marine Research, Wageningen University and Research, PO Box 77, Yerseke 4400 AB, The Netherlands

⁵Deltares, Marine and Coastal Systems, Rotterdamseweg 185, PO Box 177, Delft 2600 MH, The Netherlands

*Corresponding author: olivier.beauchard@nioz.nl

ABSTRACT: Biological traits of benthic macroinvertebrates from a large area of the North Sea soft sediments were used to explore habitat occupancy within seascapes of contrasting hydrodynamics. The area, the Dutch sector of the North Sea, is mainly composed of 2 habitats: shallow dynamic bottoms of heterogeneous geomorphologies and deep homogeneous muddy bottoms. Higher within-habitat heterogeneity was hypothesized to more specifically select benthic life strategies according to environmental filtering, i.e. through the action of abiotic forces. Functional community patterns were explored through the RLQ method, which relates habitat and trait variables, at different spatial scales of specific seascape heterogeneity, and functional diversity indices were used to shed light on community assembly mechanisms. Locally, 3 associations between habitat characteristics and biological traits were shown to correspond with predictions of life history theories, whereas only 2 emerged when considering all types of seascapes. This spatial scale-dependence was explained by abiotic alternations masked over the larger scale at which all the existing strategies could not be properly disentangled. The relative composition in strategies obeyed specific assembly rules as identified by functional diversity indices. Seascape geomorphology was locally discriminant of functional patterns, and could account for biodiversification, much beyond basic taxonomic counts. Whereas habitats of higher physical stability hosted the taxonomically richest communities, stress or disturbance frequency increased functional variations within communities due to different strategist habitat occupancies. This study proposes a generic mechanism of benthic community structuring in soft sediment shelves.

KEY WORDS: Benthic macroinvertebrate · Biological trait · Life strategy · Assembly rule · Spatial contingency · Stress · Disturbance · Geomorphology

1. INTRODUCTION

The use of biological traits has become essential to provide sound mechanistic understanding of patterns in species community ecology (McGill et al. 2006). During the last 15 yr, the use of traits in marine ecology has received growing attention, with a productive series of works on various aspects reviewed by Beauchard et al. (2017). At present, benthic macroinvertebrates are by far the most studied ecosystem component with traits, since the benthos ensures many ecological functions in the sea floor and provides diverse fundamental and applied research opportunities. For several decades, the use of traits expressing the relations between organisms and sediments ('effect traits'; Lavorel & Garnier 2002) has been central in major achievements of marine benthic ecology (Rhoads 1974, Pearson & Rosenberg 1978, Solan et al. 2004, Norling et al. 2007, Hewitt et al. 2008, Belley & Snelgrove 2016). More recently, broader perspectives have fostered the use of a wider panel of traits, including growth and reproduction, for studying the relationships between habitat characteristics and community composition (Bremner et

al. 2006, Oug et al. 2012, Fleddum et al. 2013, Darr et al. 2014), functional diversity (Bremner et al. 2003, Törnroos & Bonsdorff 2012, Villnäs et al. 2018) and also human-mediated sea floor damages and indicator development (Tillin et al. 2006, Bolam & Eggleton 2014, Bolam et al. 2017, Kenny et al. 2018, Beauchard et al. 2021).

Curiously, the specific use of traits in an evolutionary perspective on identifying life strategies has been much more limited, unlike in terrestrial ecology and limnology (Beauchard et al. 2017). In an organism, a life strategy is a suite of trait modalities that have evolved through the natural selection of abiotic forces and biotic interactions (Stearns 1992). Such traits are necessarily ‘response traits’ that express the fitness components (growth, survival and reproduction; Lavorel & Garnier 2002), and their modalities are organised in trade-offs due to constraints in energetic allocations in one or the other fitness component (Braendle et al. 2011). The concept of life strategy gained momentum with the advent of gradient theories from the 1970s with the aim at building periodic tables of living forms based on adaptations to environmental variability (Grime 1977, Southwood 1977). Growing interests in assembly rules that determine trait similarity within a community of coexisting species then deepened developments (Keddy 1992, Weiher & Keddy 1995). Through environmental filtering, abiotic forces remove species lacking specified combinations of trait modalities, inducing trait convergences into life strategies, whereas lesser abiotic control leads to trait divergence resulting from increased biotic interactions (‘limiting similarity’, MacArthur & Levins 1967). Since then, in a wide array of ecosystems, universal life strategies have been recognised to be specific of habitat spatio-temporal characteristics (Grime & Pierce 2012). For instance, *r*- and *K*-strategies are considered the respective adaptive endpoints of a gradient of decreasing disturbance frequency or magnitude in both terrestrial (Pianka 1970) and marine ecosystems (Pearson & Rosenberg 1978); individual growth and population turnover are the main characteristics of these strategies, i.e. fast and slow, respectively.

Another strategy is expected where adversity generates stress, considered for plants by Grime (1977) (‘stress resistance’) and more generally discussed by Greenslade (1983). Disturbance is here considered to be any discrete event that temporarily disrupts the structure of a habitat (Sousa 1984), whereas stress or adversity is defined as continuous environmental harshness pushing physiological limits forward (Greenslade 1983). The most recent and synthetic considerations on life strategies were largely derived from the advance of fisheries sciences and distinguish 4 strategies through the ‘precocial-opportunist-survivor-episodic’ (POSE) concept as combinations of juvenile and adult mortalities (Kindsvater et al. 2016). Whereas the opportunistic and precocial categories (high adult mortality in both; low and high juvenile survival, respectively) are respectively equivalent to *r*- and *A*-strategies, episodic and survivor are 2 distinct strategies within the *K*-strategy (both long-lived, with high and low juvenile mortality, respectively).

Although the importance of environmental filtering has been recently reconsidered (Cadotte & Tucker 2017, Thakur & Wright 2017), dominant abiotic structuring of marine benthic communities is expected (Snelgrove & Butman 1994). Water movements in the marine environment sustain strong physical forces through horizontal tidal currents and vertical wave energy transmission that directly affect the sea floor (Hall 1994). In soft sediments, this hydrodynamism, at the basis of ecological succession following physical disturbance, has channelled a long series of works investigating species functional types over spatial changes, holding applicable to chemical disturbance through time (Pearson & Rosenberg 1978, Rhoads & Germano 1982, Nilsson & Rosenberg 2000). Disturbance magnitude, recruitment and community recovery have been the main focusses in this research line (McCall 1977, Santos & Simon 1980, Levin 1984, Barry 1989, Günther 1992, Norkko et al. 2006, Sepúlveda & Valdivia 2017, Gladstone-Gallagher et al. 2021). However, most studies were based on limited spatial extents and restrained to few biological features typical of *r*- and *K*-strategies (i.e. opportunistic/pioneer vs. climax). In recent works involving a larger panel of traits (see first paragraph), the exploration of assembly rules has been largely absent; more specific perspectives on benthic life strategies were applied (Kostylev & Hannah 2007, Darling et al. 2012), but empirical relationships between traits and field data are still lacking to support the evidence of trait convergences into life strategies. Comprehensive investigations on assembly rules should take place at relatively large spatial scales at which higher habitat heterogeneity better enables the detection of environmental filtering (Weiher & Keddy 1995, Winemiller et al. 2015, Cadotte & Tucker 2017) and should involve large sets of response traits of offspring and adult stages to better account for the wider panel of life strategies (Winemiller et al. 2015).

However, the detection of different life strategies in a given area can be spatial scale-specific according to the phenomenon of ‘spatial contingency’ (Peres-Neto et al. 2012). Habitat heterogeneity is contingent upon the spatial extent under investigation so that environmental filtering may not be optimal at any spatial scale. In this respect, spatial scale-dependent patterns in benthic functional assemblages should be particularly expected on soft sediment shelves where strong abiotic dynamics shape prominent geomorphological structures of variable spatial extent that create various abiotic contrasts (e.g. tidal velocity, sediment type) at different scales (Huntley et al. 1993, Borsje et al. 2009). In marine benthic ecology, the role of geomorphology has received increasing attention (Baptist et al. 2006, Erdey-Heydorn 2008, Damveld et al. 2018, Holzhauser et al. 2020), but its role in determining associations between abiotic characteristics and organism living modes remains unknown.

In this paper, we explore the relationships between habitat characteristics and biological traits of benthic communities from a large area of the North Sea soft sediments. As a first hypothesis, we assumed that combinations of habitat characteristics should directly select specific combinations of biological traits as life strategies resulting from assembly rules. Then, given the variable geomorphological contrasts encountered on soft sediment shelves, we hypothesized that life strategies should be better discriminated under the highest habitat heterogeneity found in the investigated area. In this way, we explored the implications of geomorphology in the process of environmental filtering as a generic mechanism of benthic community structuring in soft sediment shelves.

2. MATERIALS AND METHODS

2.1. Study area

The study area, the Dutch sector of the North Sea, covers 57000 km² (Exclusive Economic Zone, EEZ; Fig. 1a). It spreads over the east half of the Southern Bight in the south and extends to the Dogger Bank in the north. Above 30 m deep, south of 54° N, currents from the eastern UK coast and the English Channel generate high bottom current speeds (>0.2 m s⁻¹) which maintain a coarse sediment mainly composed of mobile sand and prominent geomorphological structures (Fig. 1b). The northern part, ‘Oyster Ground’, is a deeper (>40 m) area characterised by lower current speeds and a much muddier sediment (Duineveld et al. 1992). Gravel beds are very sparse, and mud content in sand is the main aspect that characterises sedimentary variations. In this cold temperate system, the average bottom water temperature ranges between 9 and 12°C.

2.2. Macrozoobenthic monitoring

We used the data from a yearly monitoring programme of the macrobenthic fauna at 103 sampling stations within the Dutch EEZ that has been coordinated by the Ministry of Infrastructure and Water Management (Rijkswaterstaat 2019) since 1995. Monitoring was continuous until 2010, after which it was conducted less frequently, with the last available data dating from 2012 and 2015 (18 yearly samplings in total). Organisms were sampled between March and June by means of a Reineck boxcorer (1 replicate; 0.068–0.078 m², 15 cm deep), sieved through 1 mm, sorted and identified to the lowest possible taxonomic level. After sieving, organisms were counted and weighed (ash-free dry weight) so that 3 densities per m² were available for analyses: individual organisms, biomass and taxa; see Daan & Mulder (2009) for more details. Data analyses were based on densities of the overall period and averaged per station.

2.3. Environmental descriptors

At each station, particulate organic matter and particulate organic carbon were obtained from a core of the first 3 cm. Habitat descriptors were completed by data from different sources: stratification (van Leeuwen et al. 2015), water depth (EMODnet Bathymetry Consortium 2018) and sediment types (Dutch Ministry of Infrastructure and Water Management 2013); primary productivity was obtained from the predictions of the General Estuarine Transport Model – European Regional Seas Ecosystem Model (Baretta et al. 1995); detailed information is provided in Table S1 in the Supplement at

res.com/ articles/ suppl/ m682 p031 _ supp.pdf. Additionally, median bottom current speed and bottom wave energy, calculated over a large part of the monitoring period (monthly basis), were provided by the Deltares Institute (Delft, The Netherlands, P. M. J. Herman, pers. obs.; Cronin 2012). These environmental variables are habitat descriptors traditionally used in marine benthic ecology and can provide a mechanistic understanding of habitat occupancy since they act directly on organism fitness. They were used to test our first hypothesis according to which environmental forces could determine specific combinations of biological traits.

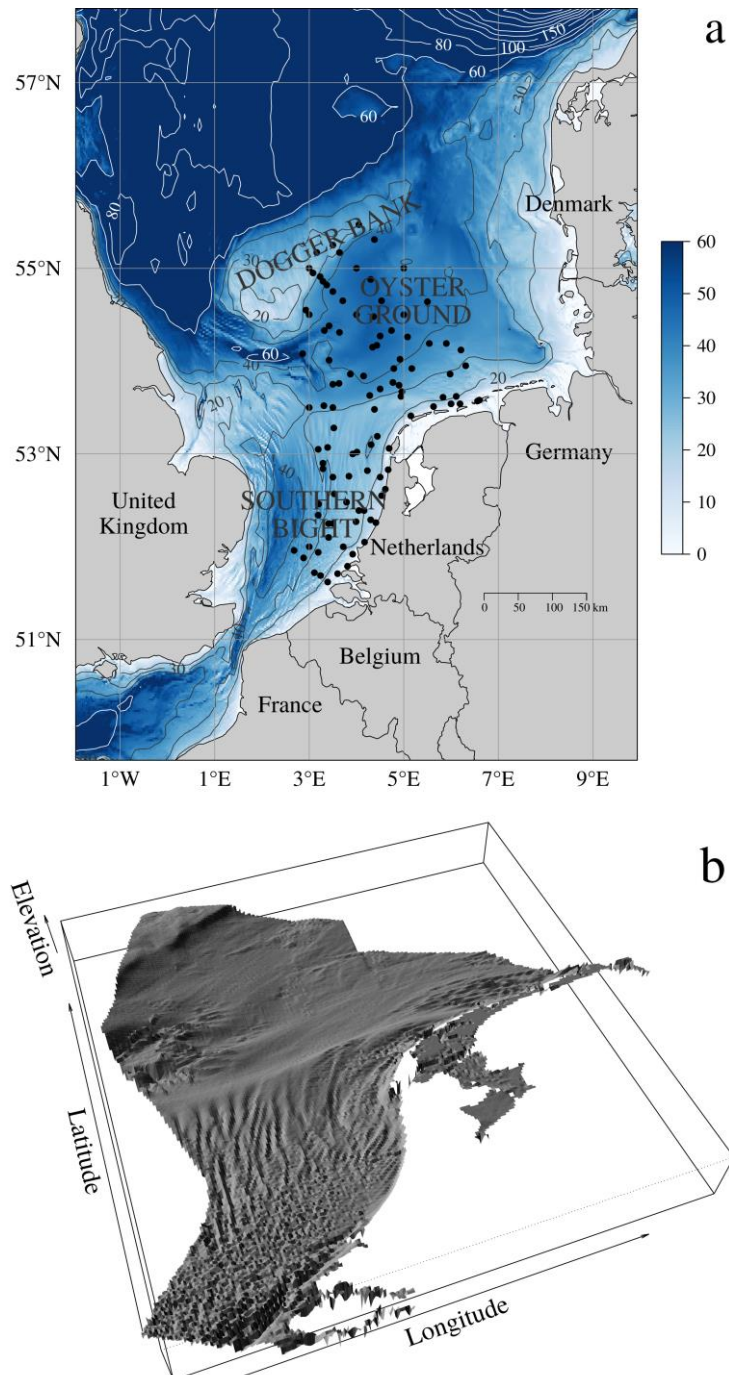


Fig. 1. (a) Study area in the North Sea. Contour lines: isobaths (m); colour bar, depth (m); black dots: sampling stations spread over the Dutch EEZ. (b) Three-dimensional bathymetric close-up of the sampled area within the Dutch EEZ displaying the geomorphological contrasts of the seascapes

Sea bed geomorphological descriptors were computed and used to underpin both hypotheses. From a bathymetric raster (resolution of 31684 m²), we considered 3 descriptors of bedforms: rugosity, representing sea floor roughness; slope as the deviation from the horizontal benchmark; and curvature as the derivative of slope. We then computed a series of bathymetric position indices (BPIs; Lundblad et al. 2006) that account for surrounding geomorphology at a defined spatial scale. A BPI expresses the elevational difference between the location of interest and the surrounding area; it was considered for radii of 800, 500, 400, 200, 100, 50, 25, 10, 5, 3 and 2 pixels, accounting for respectively 142.142, 88.829, 71.071, 35.536, 17.768, 8.884, 4.442, 1.777, 0.888, 0.533 and 0.355 km. A negative BPI indicates that a sampling station is located in a concavity such as trough, whereas a positive value indicates convexity, such as a bank.

2.4. Biological traits

Fifteen traits were considered to explore living modes of benthic organisms (Tables S2 & S3). These traits cover the major functions that express fitness components (growth, survival and reproduction) in response to environmental influences (biotic and abiotic). Data were compiled from 502 sources, mostly published peer-reviewed articles (455) and books (17) with additional grey literature (17 academic theses, 10 reports) and a few records from online data bases (3). We gave priority to works on natural history that could document traits that we considered relevant in terms of fitness expression. Traits comprised ordinal and nominal descriptors that were all qualitatively coded with the modality summarizing the main biological mode within each trait (complete disjunctive coding).

The proportion of documented taxa is a recurrent issue in trait analyses. In this study, the whole fauna was composed of 391 taxa, whereas only 190 were completely documented for traits. We assessed the relevance of the documented faunal data subset by correlation analyses. We compared number of taxa, total individual and biomass densities, calculated per sampling station, separately for the whole data set and for the documented data subset. The 3 indices were significantly and strongly correlated ($r > 0.96$, $p < 0.001$; Fig. S1). Although the number of taxa was substantially lower in the subset documented for traits, individual and biomass densities represented 92 and 96% of the whole data set, respectively. From there, we assumed that the documented subset was structurally representative of the whole data set.

2.5. Data analysis

2.5.1. Habitat identification

Large-scale abiotic contrasts are known to occur in the study area (Duineveld et al. 1992; Fig. 1b), so that in a first analysis, we combined habitat descriptors and fauna to highlight the main community gradients and to derive habitats of different abiotic heterogeneity for further specific biological trait analyses. Firstly, after \ln -transformation, faunal data were processed by correspondence analysis, and habitat descriptors, comprising a mix of quantitative and qualitative variables, were subject to Hill and Smith analysis (Hill & Smith 1976), after which both were combined into a co-inertia analysis (Dray et al. 2003). Whereas depth and wave energy conserved a strong degree of correlation independently of spatial scale, their linear relationships with current speed were strongly scale-dependent. Hence, these 3 descriptors were transformed into categorical variables (each as a series of binary variables) in order to circumvent consequent non-linear constraints. This procedure, although not commonly encountered in the ecological literature, has been known for a long time as a solution to such constraints in multivariate data analysis since relationships between binary variables are necessarily linear (Escoufier & Pagès 1990, Michailidis & de Leeuw 1998, Nishisato 2006). Co-inertia axes encompass the covariant information between habitat descriptors and fauna so that they express habitat preferences quantified by the RV-coefficient, a multivariate equivalent of the Pearson's r -coefficient (Robert & Escoufier 1976). Habitats were derived from a hierarchical clustering based on Ward's aggregation criterion (Murtagh & Legendre 2014) applied on a Euclidean distance matrix built from the co-inertia axis scores of the sampling stations.

2.5.2. Relationships between habitat descriptors, biological traits and functional diversity indices

In order to test our first hypothesis, we analysed the relationships between habitat descriptors and biological traits that should take place under environmental filtering, over the whole study area and within habitats. We applied RLQ analysis (Dray & Legendre 2008), which builds axes maximizing squared covariances between habitat descriptors (table R, defined on stations) and biological traits (table Q, defined on species) through the faunal link (table L, stations \times taxa) processed by correspondence analysis; prior to RLQ, table R was processed by Hill and Smith analysis and table Q by multiple correspondence analysis (Tenenhaus & Young 1985). The degree of association between table R and table Q is quantified by RLQ inertia, which is the fourth-corner statistic from Dray & Legendre (2008) whose significance under the null hypothesis is tested by row permutations of table L to break the link with table R (model 2) and column permutations to break the link with table Q (model 4). Significances of specific associations between habitat and traits were tested by the procedure from Dray et al. (2014) which combines variables (of tables R and Q) and RLQ axes through the fourth-corner method. Given the multiplicity of tests, a p-value adjustment was done following the false discovery rate method, accompanied by a necessarily very large number of random permutations (99999). Relationships were considered significant when p-values of both model tests were verified to be <0.05 (ter Braak et al. 2012).

The RLQ method enables the simultaneous projection of habitat descriptors and traits on the same axes, but also sampling stations and species. Hence, species RLQ axis scores can be considered as synthetic biological traits, expressing only the significantly functional part of the biological data. These scores were used to compute functional diversity indices to verify assembly rules of species coexistence in the synthetic trait space within communities, since pioneer works (see Introduction) predicted trait convergence (i.e. species close to each other) under environmental filtering (or ‘underdispersion’; Weiher & Keddy 1995). We considered the most independent indices: functional richness, evenness, divergence and dispersion (Villéger et al. 2008, Laliberté & Legendre 2010). These indices, computed per station, were simply used in a correlative way with RLQ axes. RLQ is unbiased compared to other approaches such as the community weighted mean and the species niche centroid that are based on weighted averages and ignore trait variations within communities, which can lead to spurious correlations between environment and traits (Peres-Neto et al. 2017). In this respect, the use of RLQ axes for computing functional biodiversity indices was methodologically unbiased, since these indices express within-community functional structure (Villéger et al. 2008).

2.5.3. Spatial variations and geomorphological implications

Lastly, to support our second hypothesis, we compared the levels of habitat heterogeneity that could maximize environmental filtering within the RLQ patterns. We quantified the extents of spatial variations of the associations between habitat descriptors and traits (hereafter called ‘ecological variations’) that accounted for habitat heterogeneity. We used the approach of Dray et al. (2012) based on Moran’s eigenvector maps (MEMs). MEMs are variables representing independent spatial variations over a surface area and ranked in descending order of spatial wavelength. They are eigenvectors obtained from the diagonalization of a spatial weighting matrix containing linkages between spatial units (i.e. sampling stations). Different functional features of the marine benthos could suggest the use of different linkage methods. For instance, applying the nearest neighbour could justify the relatively important sedentary living mode of benthic macroinvertebrates, whereas other methods involving more links could justify larval dispersal over large extents. As a compromise, we used the Delaunay triangulation. Significant RLQ axis station scores were then modelled through redundancy analysis (RDA) based on the forward selection of MEMs according to Blanchet et al. (2008). Finally, we compared the relative contributions of large- and small-scale MEMs to total explained RLQ variation (adjusted R^2) for each analysed spatial extent.

Within each RLQ pattern, geomorphological descriptors, unlike habitat descriptors, were assumed to be indirect drivers of species distributions so that they were passively used through correlations with the RLQ axes in order to verify if scale- and shape-specific bed forms could explain ecological variations. Most of the geomorphological descriptors took negative and positive values, and several exhibited right-skewed distributions. Prior to analyses, they were ln-transformed after having been rescaled between 0 and 1.

All analyses were performed in R 4.0.3 (R Core Team 2020): multivariate ordinations and permutation tests with the package ‘ade4’ (Chessel et al. 2004, Dray et al. 2007), functional diversity indices with ‘FD’ (Laliberté et al. 2014) and MEM computations and forward selections with ‘adespatial’ (Dray et al. 2018).

3. RESULTS

3.1. Ecological gradient and habitat description

Co-inertia analysis (Fig. 2) highlighted a main axis encompassing 99% of the variance of habitat descriptors and 99% of the variance of taxa distributions; the 2 multivariate structures being strongly correlated (best correlation obtained with organism individual density; RV-coefficient = 0.70, $p < 0.0001$). Table 1 displays correlations of habitat descriptors on the axis, which reflected a physico-chemical gradient from low dynamics in the central-northern parts (Oyster Ground area; deep, with low current speed and wave energy, and muddy and organic sediment) to high dynamics in the Southern Bight (shallow, with high current speed and wave energy, and coarse sediment). To a lesser extent, the water column was permanently mixed in the south and seasonally stratified in the north. This latitudinal gradient was not entirely monotonous as, in the northernmost part, the Dogger Bank exhibited high axis scores (Fig. 2). Although experiencing low current speed, the shallow sea floor of the Dogger Bank was substantially exposed to wave energy that maintained a sandy sediment of lower organic content. The clustering of station axis scores (Fig. 2) clearly expressed this habitat dichotomy, distinguishing the deep central-northern part (low dynamics) from the southern shallow part including the rise of the Dogger Bank (high dynamics).

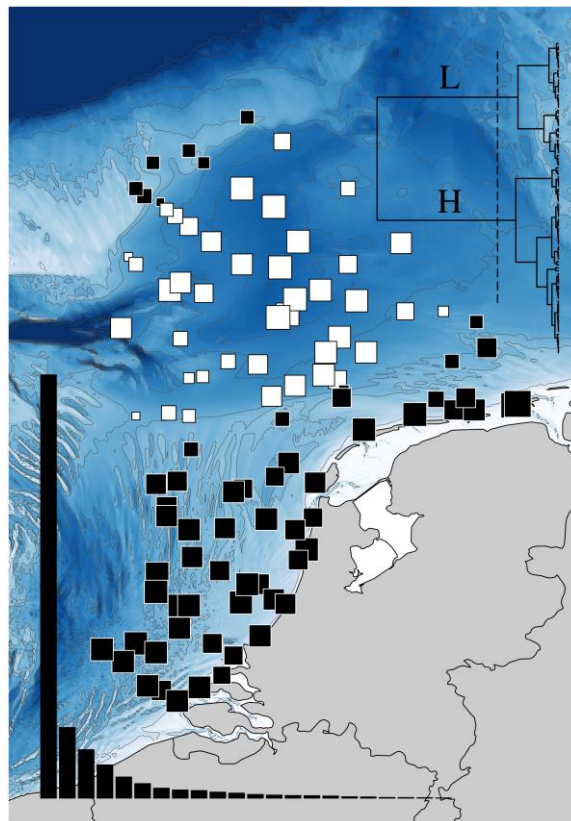


Fig. 2. Co-inertia analysis combining habitat descriptors and taxon distributions. The bar diagram illustrates eigenvalues, showing a major first axis (64%). Squares represent the first axis score of the sampling stations. White squares: low scores; black squares: high scores; square sizes are proportional to the deviation from the mean axis score [0 0]. The dendrogram shows sampling station axis score clustering; ‘L’ and ‘H’: low and high dynamics, respectively. The L-cluster includes only negative axis scores (white squares), while the H-cluster includes only positive axis scores

Table 1. Co-inertia analysis combining habitat descriptors and taxon distributions; Pearson's *r* correlations between habitat descriptors and the first co-inertia axis. Descriptors are arranged in increasing order of correlation value. TR: transitional; SS: seasonally stratified; IS: intermittently stratified; PM: permanently mixed; FI: freshwater influence. See Table S1 for detailed information on descriptors

Descriptor	<i>r</i>	<i>p</i>
Particulate organic carbon	-0.80	< 0.001
Depth – Very deep	-0.72	< 0.001
Particulate organic matter	-0.67	< 0.001
Sediment – Muddy	-0.64	< 0.001
Wave – Very low	-0.61	< 0.001
Current speed – Very low	-0.60	< 0.001
Wave – Low	-0.54	< 0.001
Stratification – TR	-0.50	< 0.001
Stratification – SS	-0.24	0.014
Current speed – Low	-0.19	0.060
Depth – Deep	-0.17	0.086
Sediment – Mixed	-0.14	0.158
Stratification – IS	0.17	0.078
Current speed – Intermediate	0.22	0.024
Depth – Very shallow	0.24	0.014
Stratification – PM	0.28	0.004
Stratification – FI	0.29	0.003
Wave – Intermediate	0.31	0.001
Sediment – Coarse	0.32	0.001
Sediment – Sandy	0.32	0.001
Depth – Shallow	0.35	< 0.001
Wave – High	0.36	< 0.001
Current speed – High	0.38	< 0.001
Current speed – Very high	0.42	< 0.001
Wave – Very high	0.44	< 0.001
Depth – Intermediate	0.47	< 0.001
Primary productivity	0.50	< 0.001

3.2. Biological trait analysis of the whole area

Over the whole area, the RLQ pattern was significant only when using organism presence–absence (Table 2). The pattern was limited to a single axis (84% of total inertia), on which the only significant correspondences between habitat descriptors and biological traits were found (Table 3).

Table 2. Summary of RLQ analyses. Number of axes: only axes on which habitat descriptors and traits are significantly related are retained for interpretation; projected inertia: variance of habitat descriptors (table R) and biological traits (table Q) expressed on RLQ axes; Chessel's correlation: fourth-corner correlation as a proportion of its optimum. Whole area and low dynamics analyses are significant only with presence–absence, high dynamics with individual organism density. See Section 2.5.2 for a description of the models

		Whole area	Low dynamics	High dynamics
Significance (<i>p</i>)	Model 2	0.00001	0.00001	0.00001
	Model 4	0.03399	0.02034	0.03692
Number of axes		1	1	2
Projected inertia (%)	Table R	96	65	88
	Table Q	75	47	70
Chessel's correlation R-Q	Axis 1	0.25	0.31	0.32
	Axis 2			0.32

The analysis reproduced the first axis of the previous co-inertia analysis without much distortion (explaining 96% of table R variance), with a similar expression of habitat descriptors (Table 3). All organism and taxonomic densities decreased from low to high dynamics (Table 3). Richer communities had larger functional volumes (functional richness) and lowest functional evenness. Functional dispersion was strongly characteristic of high dynamics, positively correlated with the first axis.

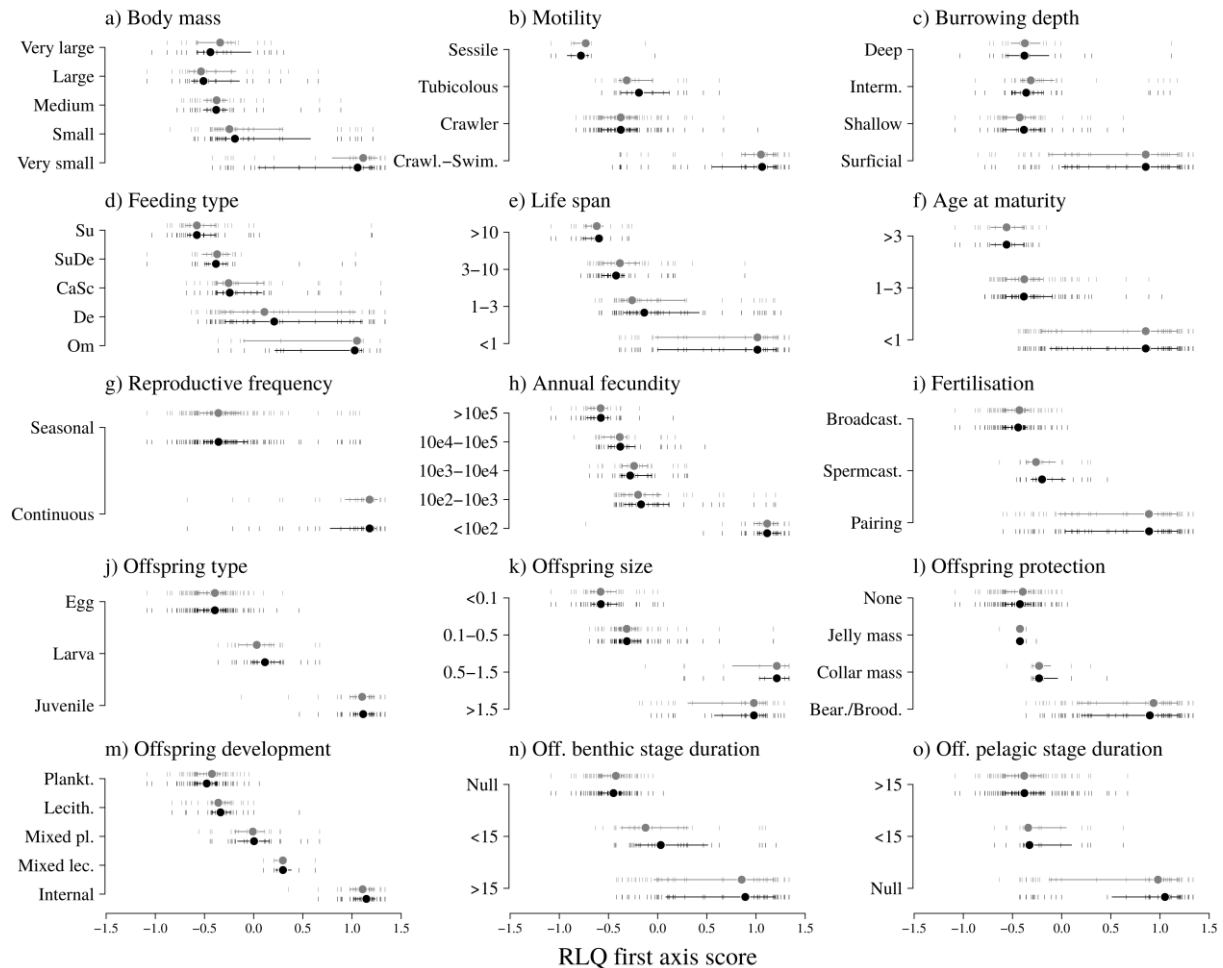


Fig. 3. Whole-area RLQ analysis, trait modality positions along the first axis. Dots, median values of species positions (vertical dashes); bars extend from 25th to 75th percentiles. Grey, low dynamics; black, high dynamics. From left to right of the RLQ axis, increase in current speed and wave energy. Feeding types are Su: suspension feeder; De: deposit feeder; CaSc: carnivore–scavenger; Om: omnivore

Out of 15 traits, 10 significantly co-structured the RLQ axis (explaining 75% of table Q variance). However, when looking at trait modality positions (Fig. 3), most of the pattern was structured by a specific set of modalities covarying together to the right side of the axis (high station scores in Fig. 2, high dynamics), in opposition to most other modalities. These were very small body mass (Fig. 3a), swimming ability (Fig. 3b), surficial living mode (Fig. 3c), earliest maturity (Fig. 3f), continuous reproduction (Fig. 3g), and release of a few large juvenile offspring after internal incubation (i.e. viviparity; Fig. 3h–m). Correlations of individual modalities with RLQ axes and their significances are provided in Table S4. These biological attributes were strongly specific to amphipods (e.g. *Ampelisca* spp., *Bathyporeia* spp., *Urothoe* spp.), isopods (e.g. *Eurydice pulchra*, *Idotea linearis*) and mysids (e.g. *Gastrosacus spinifer*, *Mesopodopsis slabberi*, *Schystomysis* sp.). Some trends in other traits appeared but remained more suggestive than significant (e.g. life span, decreasing toward high dynamics).

Table 3. RLQ analyses, significance of variables on the axes. Traits and habitat variables were tested according to the fourth-corner method combined with RLQ from Dray et al. (2014). Reported statistics (‘Stat.’) are pseudo-F for qualitative variables (depth, current speed, wave energy, stratification, sediment and each trait) and Pearson’s r for quantitative variables (all other variables); see Tables S1 & S2 for detailed information on habitat and trait variables, respectively. Relationships of geomorphological descriptors with RLQ axes were assessed by Pearson’s r; within parentheses, radius based on which bathymetric position indices (BPIs) were calculated. Missing values, encountered for small BPIs, indicate that there was no variation in the descriptor (0 as unique value), preventing computation; for functional divergence, there is no possible calculation for unidimensional space

Data	Variable	Whole area		Low dynamics		High dynamics			
		Axis 1		Axis 1		Axis 1		Axis 2	
		stat.	p	stat.	p	stat.	p	stat.	p
Habitat	Depth	18.658	0.00413	2.479	0.04660	21.012	0.01347	17.046	0.02092
	Current speed	19.494	0.00413	1.360	0.26278	27.171	0.00368	14.381	0.03511
	Wave energy	20.136	0.00413	3.547	0.01883	16.989	0.02092	11.477	0.04796
	Stratification	11.035	0.00462	3.543	0.00553	5.826	0.09244	6.077	0.04796
	Sediment	15.483	0.00413	10.525	0.00016	2.326	0.47857	8.480	0.01555
	Particulate organic matter	-0.082	0.00987	-0.044	0.03325	0.005	0.85834	0.040	0.11620
	Particulate organic carbon	-0.106	0.00817	-0.093	0.00027	-0.094	0.01074	0.006	0.85834
	Primary productivity	0.080	0.00802	-0.010	0.62008	0.055	0.04018	-0.081	0.00346
Traits	Body mass	9.815	0.04467	0.895	0.53690	15.891	0.00057	10.600	0.00943
	Motility	26.099	0.00045	4.994	0.00510	32.779	0.00006	6.769	0.09295
	Burrowing depth	24.461	0.00052	3.963	0.00851	20.794	0.00027	4.220	0.25289
	Feeding type	5.988	0.23410	0.597	0.70183	13.626	0.00152	3.997	0.26460
	Life span	8.579	0.09791	0.608	0.66929	10.622	0.01968	21.525	0.00017
	Age at maturity	15.143	0.02813	0.083	0.91250	11.644	0.02890	30.715	0.00019
	Reproductive frequency	88.792	0.00030	10.866	0.00232	34.502	0.00152	15.160	0.03305
	Annual fecundity	8.362	0.08762	3.506	0.00840	25.318	0.00006	4.895	0.17303
	Fertilization	21.711	0.00514	5.369	0.00844	20.317	0.00172	3.090	0.35027
	Offspring type	24.888	0.00168	2.990	0.08151	48.120	0.00006	7.727	0.09168
	Offspring size	14.473	0.01279	5.849	0.00150	24.459	0.00010	3.811	0.28190
	Offspring protection	17.071	0.00514	7.074	0.00150	6.979	0.09295	8.923	0.04688
	Offspring development	20.391	0.00050	3.512	0.01060	20.006	0.00006	6.727	0.07967
	Offspring benthic stage duration	10.294	0.09448	7.434	0.00150	22.298	0.00112	21.849	0.00115
	Offspring pelagic stage duration	6.311	0.25477	0.121	0.91250	40.818	0.00006	1.800	0.53427
Community	Individual density	-0.463	<0.00001	0.042	0.79389	-0.392	0.00164	0.229	0.07361
	Biomass density	-0.267	0.00649	-0.520	0.00049	-0.696	<0.00001	-0.148	0.25113
	Taxonomic richness	-0.697	<0.00001	0.113	0.48213	-0.186	0.14782	0.598	<0.00001
	Functional richness	-0.703	<0.00001	-0.484	0.00135	-0.288	0.02297	0.155	0.22975
	Functional evenness	0.673	<0.00001	-0.359	0.02111	-0.424	0.00060	-0.002	0.99016
	Functional divergence					0.227	0.07637	-0.377	0.00256
Functional dispersion	0.747	<0.00001	0.668	<0.00001	0.424	0.00060	-0.174	0.17602	
Geomorphology	BPI 02 (355 m)	0.138	0.16434			0.180	0.16230	-0.140	0.27683
	BPI 03 (533 m)	0.110	0.26714			0.117	0.36379	-0.133	0.30416
	BPI 05 (888 m)	0.099	0.31933			0.220	0.08611	-0.011	0.92952
	BPI 10 (1777 m)	-0.029	0.76955	0.245	0.12214	0.044	0.73366	0.148	0.25157
	BPI 25 (4442 m)	-0.048	0.62795	0.104	0.51720	-0.057	0.65720	0.157	0.22279
	BPI 50 (8884 m)	-0.036	0.71632	-0.021	0.89558	-0.135	0.29571	0.176	0.17042
	BPI 100 (17768 m)	0.022	0.82265	0.237	0.13521	-0.245	0.05531	0.110	0.39586
	BPI 200 (35536 m)	0.220	0.02572	0.297	0.05931	-0.338	0.00714	-0.119	0.35594
	BPI 400 (71071 m)	0.470	<0.00001	0.548	0.00021	-0.411	0.00091	-0.204	0.11213
	BPI 500 (88750 m)	0.543	<0.00001	0.567	0.00011	-0.496	0.00004	-0.218	0.08826
	BPI 800 (142142 m)	0.570	<0.00001	0.534	0.00032	-0.543	0.00001	-0.149	0.24849
	Rugosity	0.263	0.00732	-0.266	0.09275	0.289	0.02249	-0.009	0.94312
	Slope	0.489	<0.00001	-0.098	0.54373	0.129	0.31662	-0.374	0.00276
	Curvature	0.072	0.46835	-0.059	0.71270	0.167	0.19461	-0.034	0.79228
	PCA axis 1	0.166	0.09344	-0.513	0.00060	-0.172	0.18069	0.010	0.94087
	PCA axis 2	0.411	0.00002	0.180	0.25918	-0.527	0.00001	-0.083	0.52037

Moreover, and apart from these specific attributes, between-habitat trait ordination was almost not affected by the abiotic differences (Fig. 3; no discrimination between grey and black distributions). This was likely explained by the lack of species specificity among the 2 habitats: 152 and 167 taxa were found in low and high dynamics, respectively, with 129 in common (only 38 not shared), illustrated by large range overlaps of the 2 faunas. By contrast, within-habitat coefficients of variation of taxon richness largely differed, with only 8% in low dynamics and 31% in high dynamics. Also, averaged individual organism frequencies per trait modality revealed noticeable differences between the 2 habitats (Fig. S2). Additional to differences in mean densities, a major feature was the systematically larger within-modality variation in high dynamics (SD = 5.26 against 2.52 in low dynamics), indicating higher

functional heterogeneity among communities in high dynamics, and advocating for within-habitat analyses.

3.3. Biological trait analysis in low dynamics

RLQ analysis on low dynamics data revealed only 1 axis significantly related to both habitat descriptors and traits (Table 2); again, only organism presence–absence yielded a significant pattern. Only 9 traits were significantly expressed and included mostly modalities identifying the peculiar biology of the small crustaceans previously highlighted in the whole-area analysis (Table 3). Due to their redundancy, the results are not further detailed, and graphical displays are provided in the Supplement (Figs. S3 & S4). However, it should be noted that a prominent second axis was found to be related to several habitat descriptors (Fig. S3), and, although not significant, a few trait modalities were differentiated on the top of this axis, characterising sessile living mode and release of large number of small eggs in the lowest dynamic conditions of the area (Fig. S4).

3.4. Biological trait analysis in high dynamics

The RLQ pattern of high dynamics was significant only when using individual densities and showed that 2 clear gradients could be considered (Table 2, Fig. 4a). The first axis identified a large extent of southern offshore stations of intermediate depth and characterised by high current speed and lower organic content (Fig. 4b). Independently, the second axis opposed shallower stations undergoing very high wave energy with higher primary productivity (lower part of the axis) to deeper muddy stations of minimum current speed and lower wave energy (upper part). This second axis was much less spatialized; lower hydrodynamics (i.e. current and wave), although characteristic of the Dogger Bank in the north, were also found patchily distributed within the most hydrodynamic extent of the overall study area (Fig. 4c). In summary, 3 sub-habitats were encountered here: stations stressed by high current speed (Fig. 4a, right and bottom-right), stations undergoing strong wave action (Fig. 4a, bottom to bottom-left) and stations of lower hydrodynamics (Fig. 4a, to the top); Fig. S5 provides detailed distributions of all habitat descriptors.

These sub-habitats were strongly characterised by benthic functionalities as all biological traits significantly corresponded to the axis scores (Table 3). The very small short-lived crustaceans identified in the whole-area analysis were typical of high current speed on the right side of the first axis (Fig. 5). In opposition, the other taxa were spread mainly along the second axis, from disturbed to more physically stable conditions. Between these latter two, disturbed conditions were characterised mainly by smaller and shorter-lived taxa (Fig. 5b,f). Tubicolous living mode was most characteristic, represented by *Capitella capitata*, *Heteromastus filiformis*, *Mediomastus fragilis*, *Polydora* sp., *Prionospio* sp., *Spio* spp. and *Pygospio elegans*. This living mode was associated with spermcasting (Fig. 5j), typical in many sedentary worms of mixed offspring development which brood their clutches for a short time until larval release (mixed lecithotrophic; Fig. 5k,m–o). These reproductive attributes were also encountered in co-occurring decapods such as *Carcinus maenas*, *Corystes cassivelaunus*, *Crangon crangon*, *Diogenes pugilator*, *Liocarcinus* sp. and *Pagurus bernhardus*, releasing large planktotrophic larvae after a long brooding incubation (mixed planktotrophic). The upper part of the axis, toward lower dynamism, was characterised by taxa of extended life span with later maturity (Fig. 5b,f,g). These characteristics were associated with reproductive modes lacking parental care, through seasonal broadcasting of numerous small pelagic eggs (Fig. 5h–l). Large bivalves were typical of this strategy, well represented by *Arctica islandica*, *Ensis* spp., *Mya* spp. and *Spisula* spp., although phylogenetically distant taxa exhibited similar combinations of attributes, like echinoderms (*Echinocardium* sp., *Acrocnida brachiata* and *Amphiura* spp.) and polychaetes (*Glycera* sp. and *Streptosyllis websteri*). There was no clearly identified feeding type here. However, suspension feeding seemed slightly more specific compared to carnivory, more centrally positioned along the second axis (Fig. 5e). Globally, there was a greater burrowing ability among the taxa from the left side of the plane than among those from areas of high current speed, mainly restricted to the sediment surface (Fig. 5d).

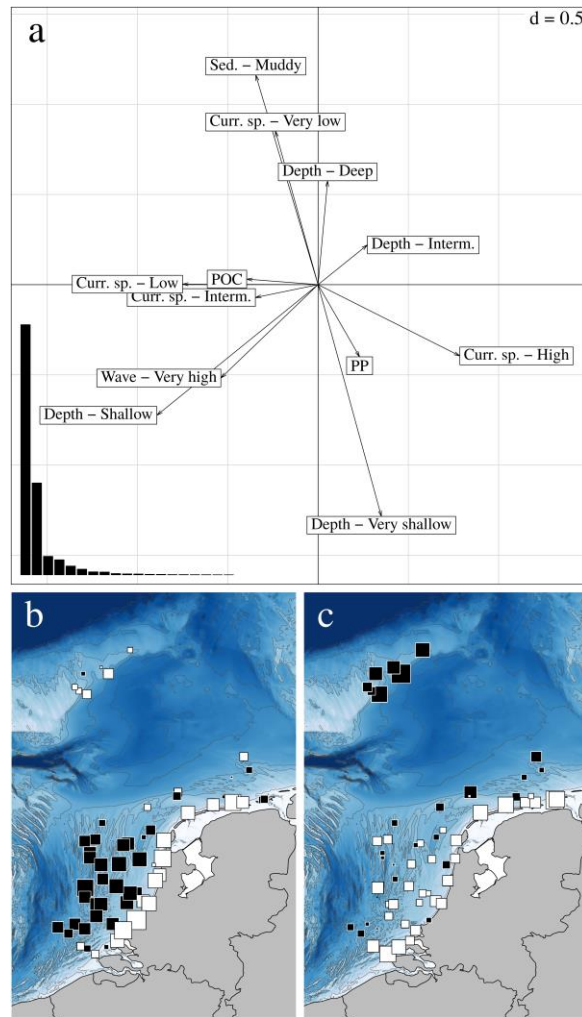


Fig. 4. RLQ analysis of the high-dynamics habitat. (a) Habitat descriptors projected onto axes 1 and 2; ‘d’ indicates the grid scale; bar diagram, eigenvalues (axis 1, 62%; axis 2, 23%); for clarity, only the significant modalities of qualitative variables are shown (according to Table S4). Curr. sp.: current speed; Intern.: intermediate; POC: particulate organic carbon; Sed.: sediment; Strat. – PM: stratification – permanently mixed; PP: primary productivity. (b) Station axis score 1. (c) Station axis score 2. White squares, low scores; black squares, high scores; square size is proportional to the deviation from the mean

Fig. 5a provides a synthetic representation of the distributions of life strategies; 4 groups were chosen for an optimal description. Typical of high current speed, group 1 represented $25 \pm 15\%$ (SD) of the average total individual density. Group 2, less functionally specific, consisted in the basis of species assemblages, representing $55 \pm 17\%$. Groups 3 and 4 accounted for 12 ± 6 and $9 \pm 13\%$ of densities, respectively. Total individual and biomass densities were limited by high current speed, and taxonomic richness increased with less physical constraints toward group 4, significantly and positively correlated only with the second axis (Table 3). In high current speed, communities were more functionally dispersed and less functionally even. Functional divergence increased from the top (lower hydrodynamics) to the bottom (wave action) of the second axis.



Fig. 5. RLQ analysis of the high-dynamics habitat. (a) Species clustering for synthetic interpretation. (b–p) Distributions of trait modalities (ellipses) respective to each trait (windows); blue dots, taxon positions; trait modalities are positioned at the gravity centre of their respective taxa. ‘d’ indicates the grid scale. Feeding types are Su: suspension feeder; De: deposit feeder; CaSc: carnivore–scavenger; Om: omnivore. See Table S2 for detailed information on trait modalities

3.5. Spatial structuring of ecological variation

The 3 RLQ patterns were significantly structured according to MEM predictions (Fig. 6a; Table S5). In spite of variable degrees of spatialization (adjusted R^2 ranging from ca. 0.7 to 0.9), a major outcome was the explanatory dominance of MEM 1 in the whole-area RLQ, compared to within-habitat RLQs. Whereas MEM 1 explained two-thirds of the variation of the whole-area pattern, it only explained ca. 10 or 30% of within-habitat patterns, for which the additions of several MEMs of higher ranks (smaller scales) were necessary to predict a substantial amount of the total ecological variation. Fig. 6b–d displays the amounts of predictions per class of spatial variation (wavelength) and shows that small- to very small-scale ecological variations dominate the within-habitat patterns compared to the whole-area pattern.

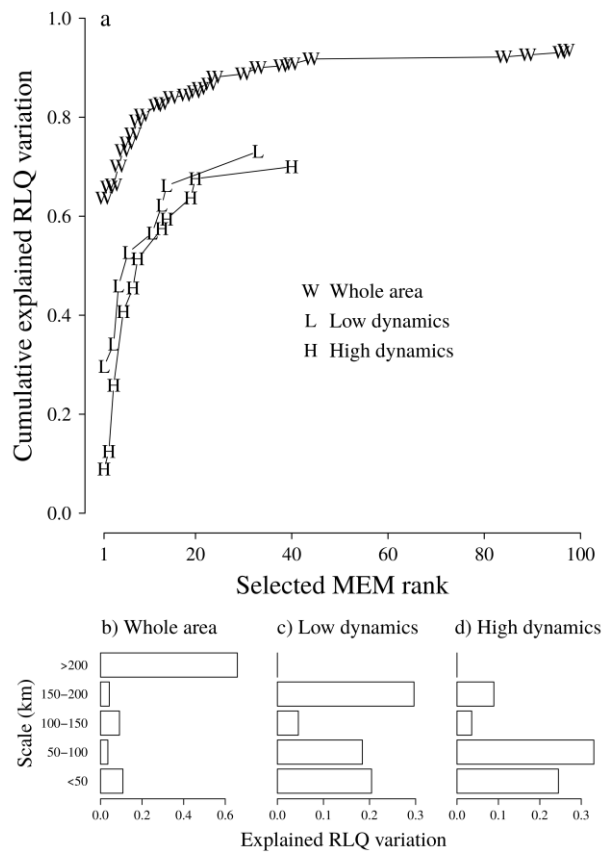


Fig. 6. Spatial structuring of RLQ patterns: (a) x-axis, Moran's eigenvector maps (MEMs) ranked by descending order of magnitude in spatial variation; y-axis, explained RLQ variation by selected MEMs (adjusted R²), and cumulated across MEMs. Note that a total of 102 MEMs are derived from the whole area that comprises 103 stations (n stations – 1); similarly, 40 MEMs are from low-dynamics areas and 61 are from high-dynamics areas; only the significant MEMs are considered here. (b–d) Explained RLQ variation by class of spatial wavelength

3.6. Relationships with seascape geomorphology

An outcome common to the 3 RLQ patterns was the large absence of significant correlations with individual small-scale BPIs (Table 3). Only large-scale ones, with slope and curvature, exhibited significant associations, as expressed by each first PCA axis (Fig. S6). However, second PCA axes from whole-area and high-dynamics habitat provided a synthetic opposition between small- and large-scale BPIs (Fig. S6a & S6c), and indicating significantly higher values of small-scale BPIs in high dynamics (right side of the first RLQ axis of both whole-area and high dynamics). Hence, these small-scale geomorphological variations were concordant with the dominant small ecological variations observed in the high-dynamics habitat (Fig. 6). This supported the role of local shelf geomorphology that indirectly generates abiotic heterogeneity, and consequently optimal environmental filtering of most diversified trait convergences (i.e. Fig. 4).

4. DISCUSSION

4.1. Importance of the type of organism density

The results showed that the type of organism density in table L can be determinant to detect significant relationships between biotic and abiotic components. In no case did biomass density lead to significant habitat–trait relationships. Over the whole area, only presence–absence enabled the detection of significant relationships given the important overlaps of species ranges and the high number of

species found in both habitats and along which taxonomic richness was more responsive than individual and biomass densities (Table 3). Similarly, the better response of presence–absence in the low-dynamics habitat can be explained by the high abiotic homogeneity, firstly, marked by the absence of 7 habitat states (Table S4). Secondly, individual organism densities per trait modality were twice more variable in the high-dynamics habitat (Fig. S2), which exhibited a more diversified abiotic pattern, and for which only individual density led to a significant RLQ pattern. In this habitat, the unique responsiveness of individual density suggests an effect of density dependence, as corroborated by its higher spatial complexity, whereby geomorphological variations may be locally more beneficial to species widely distributed across the seascape. The absence of responsiveness from biomass density is consistent with the work of Bijleveld et al. (2018), who did not find any strong relationship between species biomass and occupancy in the Wadden Sea, a highly dynamic system at the southeastern edge of our study area; the authors speculated that biomass might be more dependent on species-specific life history constrained by temporal unpredictability such as adult survival and recruitment success (Beukema 1982). Our outcomes suggest that demographic processes (i.e. individual density) may be more determinant than production (i.e. biomass density) in benthic functional patterns as concluded by Bolam et al. (2002). Nevertheless, as shown in the high-dynamics pattern, total biomass community, negatively correlated to the first RLQ axis, can be indicative of a stress effect on biological production (Table 3).

4.2. Benthic life strategies

In each of the 3 RLQ analyses, the first axis captured the main functional singularity of the patterns, clearly discriminating the small surface-dwelling crustaceans, identified as group 1 in the high-dynamics analysis. The taxa from this group have a very small biomass and they generally do not exceed 1 cm in body length. Their fecundity is minimal, as direct development leads to the release of juveniles larger than 1 mm, which translates a large reproductive allocation during a short life in an environment exposed to predation. This ensures a high juvenile survival rate that compensates for high adult mortality as encountered in amphipods (Sainte-Marie 1991). This fast living mode was systematically associated with high current speed from the sandy bottom. Experimental evidence confirmed strong adaptations of amphipods to high current speeds and catastrophic drift through physical displacement (Grant 1980), supported here by strong swimming ability in group 1 (Table 3, Fig. 5c; Table S4). Affinity of these organisms for mobile sands has been reported in other shallow coastal areas (Dahl 1952, Sameoto 1969, Oliver et al. 1980) as well as on deep continental slopes (Thistle et al. 1985). These observations suggest the concept of *A*-strategy, achieving reproductive success as fast as possible given adverse conditions (Greenslade 1983). Although this group was taxonomically very homogeneous (i.e. mostly amphipods, cumaceans and mysids), it comprised 1 non-crustacean taxon, the brittle star *Amphipholis squamata*, exhibiting similar growth and reproductive features and also found in high dynamics, suggesting a functional convergence despite phylogenetic distance.

A-strategy was detected at the 2 investigated scales, whereas local habitat heterogeneity was necessary to detect other strategies, especially along the second RLQ axis of the high-dynamics pattern. Unlike group 1, isolated by very specific trait modalities, the other groups were arranged along the second axis following a biological continuum, opposing 2 extreme and more familiar functional types according to the *r*- to *K*-selection continuum (Pianka 1970), from group 3 to group 4, respectively. Although the properties of these strategies can be widely variable and even confusing in the ecological literature, life span and associated age at sexual maturity are typically able to discriminate *K* from *r*. Also, body size is generally considered to be correlated to these traits, but body mass modalities, even if significant on both axes, were not perfectly positioned in an ordinal way along the second axis (Fig. 5b). However, growth rate, a concurrent correlate of the *r*–*K* concept, available for 76 taxa, was significantly and negatively correlated to the second axis (Fig. S7; $r = -0.51$, $p < 0.001$), whereas no link appeared with the first axis ($r = 0.10$, $p = 0.411$). Indeed, relatively short-lived species from group 3 could exhibit remarkable sizes among crabs (e.g. *C. maenas*) and nereid worms (e.g. *Alitta virens*); by contrast, the charismatic North Atlantic quahog *Arctica islandica* from group 4, of comparable body mass, does not reach the age at maturity before 5–10 yr old, more than the life span of the 2 former species. Reproductive traits have also been considered discriminant of the 2 strategies, like high fecundity in *r*-strategists and low fecundity with parental care in *K*-strategists in general (Southwood 1977, Greenslade 1983) and more specifically in the marine benthos (Giangrande et al. 1994, Ramirez

Llodra 2002). Our results are contradictory, since fecundity suggests an increasing trend from group 3 to group 4, at least along the first axis (Fig. 5i), and more costly parental care in *r*-like taxa (Fig. 5m). Here, we argue that these historical and influential considerations were built on generalities either restricted to terrestrial ecology or mainly derived from fish ecology that may have been limited, especially in the absence of empirical evidence in the marine benthos. This requires some clarification based on new advances in the field.

Whereas *A*-strategists (group 1) are equivalent to the precocial type of the POSE concept (Kindsvater et al. 2016), the *K*-like taxa (group 4) are very consistent with the episodic type: large bodied and broadcasting large numbers of small eggs, with consequently a high offspring mortality, whereas larval settlement followed by successful slow growth leads to greater adult survival. This is typical in long-lived bivalves (Beukema et al. 2001, Ridgway & Richardson 2011, Gerasimova & Maximovich 2013), including those positioned in the upper section of our *r*-*K* axis. Given the high offspring vulnerability, successful reproduction is rarely achieved, which requires an extended life span to ensure a minimum number of successes when environmental stochasticity (e.g. temperature, planktonotrophy, predation) enables it. Our results indicate that late sexual maturity is a correlate of this strategy, although long-lived (>10 yr) *Chamelea striatuala*, *Dosinia* spp. and *Mytilus edulis* can already spawn at 1 to 2 yr old; similarly, *Echinocardium* sp. (mainly represented by *E. cordatum*), matures at 3 yr in the North Sea, but at only 2 yr old further south. On the first axis opposing *A*- to *r*- and *K*-types, and suggestively along the second axis, suspension feeding also converges to an episodic adaptation in intermittently available food resource known to induce episodic reproductive success over the long term (Beukema et al. 2001).

Conversely, taxa from group 3 exhibited characteristics of *r*-strategy of which fast growth is most indicative. Also, tubicolous and other worms encountered in this group (capitelids, nereids, spionids) are known to persist in disturbed environments by optimizing recruitment during their short life. As indicated in our results, a typical reproductive feature of these taxa is the release of benthic jelly egg masses (that can be brooded inside tubes) through mixed development. This provides protection on the sea floor until an advanced larval stage emerges in the plankton once mortality rate is minimized (Pechenik 1990), after which a brief lecithotrophic pelagic stage, lasting from a few hours to a few days, avoids dispersal too far from the right habitat at the right time (Bhaud & Duchêne 1996). Taxa like *C. capitata*, *H. filiformis*, *Kurtiella bidentata*, *Mediomastus fragilis*, *Polydora* sp. and *Spio* spp., which are highly abundant in early ecological succession stages, are known to massively colonize disturbed and defaunated environments (Diaz & Rosenberg 1995). Most of the taxa of group 3 have been reported as either opportunistic or pioneer following disturbance and are consequently *r*-selected species (Grassle & Grassle 1974, Pearson & Rosenberg 1978, Rhoads et al. 1978, Reise 1982). Recruitment in such taxa can be paced by seasonally predictable wave height or ensured against inter-annually unpredictable disturbance through other attributes such as an extended spawning season (Grassle & Grassle 1974, Barry 1989). In their thorough review on marine benthic life strategies, Giangrande et al. (1994) proposed ontogenetic development as a determinant of the *r*-*K* concept. Progenesis and neoteny were hypothesized to be indicative of, respectively, *r*- and *K*-strategies, but our results indicate the opposite in regard to dominant oviparity in *K*, and manifest release of larger offspring in advanced stages of development in *r*, with the most extreme neoteny in the *A*-strategy. Additionally, high fecundity, usually associated with progenesis, has been considered to be characteristic of the *r*-strategy, contradicting Fig. 5i, which suggests the opposite. Our results are consistent based on energetic considerations whereby offspring protective allocation should be achieved at the expense of fecundity as evidenced in marine fishes ('periodic' type; Winemiller & Rose 1992) and spotlighted by Giangrande et al. (1994) as an alternative model for the benthos. Moreover, the presence of the shore crab *C. maenas* in group 3 contrasts the results given its high fecundity (>10⁵ larvae), but its growth rate and remaining reproductive attributes confer it the particular nature of opportunistic species and successful invader (Audet et al. 2008). More generally, *r*-selected species dwell in highly variable environments where population size and recruitment can be poorly correlated (Kindsvater et al. 2016), so that minimum offspring advantage (protection or release at an advanced stage) must be required to ensure the persistence of the population in the long term.

Regarding the POSE concept, the question of the survivor strategy, indiscernible in our results, remains. Even though taxa from group 4 (*K*-like) exhibited key determinants of this strategy (slow growth, late maturity, long life, large body), their excessive fecundities and protogenic ontogeny did not match expectations of survivors for which both adult and offspring mortalities are low (Kindsvater et al.

2016). For instance, *Nephrops norvegicus*, found in low dynamics, is a slow-growing species that also provides substantial parental care (brooding) at the expense of fecundity (10^3 – 10^4 released larvae). However, this species was found only twice, since the boxcorer is not designed to capture such a large organism. By extension, we could speculate that in benthic marine invertebrates, survivors can be found mostly in the mega-benthos. Associating mega-benthos may help concluding on body size for which distinctions between r and K were not clear in our results. At least, in the absence of adapted survey data, our findings suitably related to the endobenthos and body size-limited epibenthos correctly match predictions of the habitat template concept (Greenslade 1983, Southwood 1988), aligned with other models such as Grime's triangle derived from vegetation ecology (Grime 1977).

4.3. Assembly rules

In general, higher organism densities and numbers of taxa were found in deeper areas of lower hydrological dynamism, consistently with the stability–time hypothesis (Sanders 1968), according to which higher physical stability enables more individual organisms to survive, consequently benefiting higher numbers of species. In the timing of a life span, disturbance frequency can modulate reproductive success by acting on key traits like age at sexual maturity, followed by some delays for ensuring effective recruitment (Lytle 2001). The species-richer low-dynamics habitat is indeed proportionally composed of twice more individual organisms of late maturity (>3 yr) or extended life span (>10 yr; Fig. S2) that characterise the episodic strategy to cope with fluctuations in food resources due to possible stratification in this deep area that can happen episodically (van Leeuwen et al. 2015). Over the whole area, low current speed and wave energy also benefitted more diverse combinations of trait modalities as indicated by higher functional richness, the community functional volume in the trait space (Table 3). This outcome is consistent with the lack of significant separation between r - and K -strategies in deep, low-dynamic habitats where both coexist.

Although the decrease in functional richness toward A -conditions over the whole area could match early expectations of environmental filtering ('trait underdispersion', Weiher & Keddy 1995), the systematic increase in functional dispersion is contradictory, A -strategists coexisting with others (e.g. group 2), hence revealing some functional heterogeneity in spite of environmental adversity. In the high-dynamics habitat, divergence (niche specialisation, how far species occur from the mean distance from the community centroid), increasing from less to more hydrodynamic conditions (either high current speed or wave action, second axis), may provide a similar explanation.

Furthermore, functional evenness (functional complementarity, opposed to redundancy) exhibited opposite trends along the first RLQ axes. Over the whole area, its increase toward A -conditions, like functional dispersion, was likely due to an increase in density in A -strategists among r - and K -strategists, complementarily filling the functional community space. In contrast, the reverse trend in the high-dynamics habitat was likely due to the omnipresence of A -strategists across the seascape and the functional diversifications in r - and K -environments on the left side of the first axis where larger r - and K -abundances balance the functional distribution. In the low-dynamics habitat, given the presence of A -strategists limited to the margins of the area (Fig. S3), the same reverse trend might be explained by additional processes. There, the presence of engineer species (e.g. *Callianassa subterranea*, *Chaetopterus variopedatus*, *Upogebia deltaura*) might facilitate space occupation across the sediment matrix by burrowing, sediment mixing and bioirrigation (Pearson 2001, Kristensen et al. 2012), benefiting various species as supported by higher functional richness. While we focussed on environmental forces that impact response traits (expressing fitness), further analyses based on effect traits would provide interesting insights on the contribution of ecological engineering to this functional filling (Snelgrove 1999, Hewitt et al. 2008, Thakur & Wright 2017).

4.4. Scale and seascape geomorphological implications

The Dutch sector of the North Sea displays geomorphological variations strongly associated with large-scale ecological variations in the whole-area pattern (first RLQ axis), as indicated by large-scale BPIs. However, the expression of these BPIs was limited to the major latitudinal depth gradient that segregated the 2 main habitats, and associations between small-scale geomorphology and small-scale ecological variations could not be clearly detected, even in the presence of prominent geomorphological

contrasts in the southern area. As a result, only 2 extreme benthic functional types were grossly detected in association with shallow high dynamics (*A*-strategy) and deep low dynamics (indistinctly *r*- and *K*-strategies). The importance of large-scale BPIs in the low-dynamics pattern was more expectable given the smoother bed morphology. There, the small-scale ecological variations could only be attributed to the slightly variable hydrology and sediment characteristics. Although the spatial resolution of the bathymetric data may have been too limited to get significant relationships with small-scale BPIs, the second BPI-PCA axis supported the association between geomorphology and life strategies in high dynamics. *A*-selected communities occurred mainly on convexities of high curvature, generally associated with higher turbulences, whereas *r*- and *K*-communities could occur in troughs, depending on slope. This pattern is corroborated by a recent small-scale study focussing on macrobenthic assemblage composition along asymmetrical sand waves (200 m long) in the highly dynamic part of the present study (Cheng et al. 2021), showing taxa typical of *A*-strategy dominating the most turbulent parts (gentle slopes and crests), whereas assemblages of other various taxa were found in the less turbulent parts (steep slopes and troughs). From the whole area to the high-dynamics patterns, the decorrelation between depth and current speed and wave energy seems to be the major explanation for the higher benthic functional complexity in high dynamics. By generating local independent changes in hydrological and sediment conditions, alternation of bed forms was the major source of small-scale ecological variations, blurred over larger scales by other types of contrasts like those in low dynamics.

In the present study, these findings reveal a spatial scale-dependence whereby the detection of all 3 life strategies depends on greater seascape heterogeneity, more locally pronounced. In this respect, our second hypothesis was supported. However, the spatial extent considered in this study does not enable us to define a universal scale at which the most divergent life strategies can be detected given the possible independence between extents of sand wave fields or sand banks and continental shelf surface area. At the least, these findings advocate for multiple applications to shed light on this point given the contingent nature of ecosystems (Belyea & Lancaster 1999, Peres-Neto et al. 2012).

4.5. Conclusions

In this study, we provided field evidence of evolutionary trait convergences in the benthos from a soft-sediment shelf, as expected through environmental filtering. However, we also showed that the likelihood of the process may not be greater at larger spatial scales as usually expected (Weiher & Keddy 1995), but may depend on spatial contingencies of habitat heterogeneity (Peres-Neto et al. 2012), with variable assembly patterns across changing scales and associated heterogeneities. Nevertheless, and contrary to current opinions (Aguilar-Trigueros et al. 2017), we showed that environmental filtering is not a relic in the marine benthos where life strategies can be clearly determined by physical forces, although we do not neglect implications of ecological engineering at smaller scales as another assembly rule; further investigations on effect traits could shed light on this point. As reflected in the outcomes of this work, the use of life strategies provides a synthetic way of interpreting species community patterns and more considerations of the concept could facilitate comparisons between studies and exchanges between benthic ecologists through a common language beyond biogeographic differences (Weiher & Keddy 1995).

Soft-sediment shelves are distributed worldwide (Harris & Baker 2020), and the immutable properties of hydrological effects on sediments may shape universal patterns of benthic synecological organisation in these marine systems, since the deterministic nature of assembly rules remains universal (Belyea & Lancaster 1999). Although ecosystems may be subject to spatial contingencies, assembly rules in soft sediment shelves might generally operate in the range of spatial scales identified in the present study, while disappearing at larger scales. In spite of the negative effects of physical forces on taxonomic diversity, hydrodynamics generate environmental characteristics that remain sufficiently contrasted to maintain a mosaic of heterogeneous benthic functioning with specific assembly rules beyond simple taxonomic counts.

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LITERATURE CITED

- Aguilar-Trigueros CA, Rillig MC, Ballhausen MB (2017) Environmental filtering is a relic. A response to Cadotte and Tucker. *Trends Ecol Evol* 32:882–884
- Audet D, Miron G, Moriyasu M (2008) Biological characteristics of a newly established green crab (*Carcinus maenas*) population in the southern Gulf of St Lawrence, Canada. *J Shellfish Res* 27:427–441
- Baptist MJ, van Dalftsen J, Weber A, Passchier S, van Heteren S (2006) The distribution of macrozoobenthos in the southern North Sea in relation to meso-scale bedforms. *Estuar Coast Shelf Sci* 68:538–546
- Baretta JW, Ebenhöf W, Ruardij P (1995) The European regional seas ecosystem model, a complex marine ecosystem model. *Neth J Sea Res* 33:233–246
- Barry JP (1989) Reproductive response of a marine annelid to winter storms: an analog to fire adaptation in plants? *Mar Ecol Prog Ser* 54:99–107
- Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecol Indic* 76:81–96
- Beauchard O, Brind'Amour A, Schratzberger M, Laffargue P, Hintzen NT, Somerfield PJ, Piet G (2021) A generic approach to develop a trait-based indicator of trawling-induced disturbance. *Mar Ecol Prog Ser* 675:35–52
- Belley R, Snelgrove PVR (2016) Relative contributions of biodiversity and environment to benthic ecosystem functioning. *Front Mar Sci* 3:242
- Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86:402–416
- Beukema JJ (1982) Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. *Neth J Sea Res* 16:37–45
- Beukema JJ, Dekker R, Essink K, Michaelis H (2001) Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Mar Ecol Prog Ser* 211:143–155
- Bhaud M, Duchêne JC (1996) Change from planktonic to benthic development: Is life cycle evolution an adaptive answer to the constraints of dispersal? *Oceanol Acta* 19:335–346
- Bijleveld AI, Compton TJ, Klunder L, Holthuijsen S and others (2018) Presence–absence of marine macrozoobenthos does not generally predict abundance and biomass. *Sci Rep* 8:3039
- Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecology* 89:2623–2632
- Bolam SG, Eggleton JD (2014) Macrofaunal production and biological traits: spatial relationships along the UK continental shelf. *J Sea Res* 88:47–58
- Bolam SG, Fernandes TF, Huxham M (2002) Diversity, biomass, and ecosystem processes in the marine benthos. *Ecol Monogr* 72:599–615
- Bolam SG, Garcia C, Eggleton J, Kenny AJ and others (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res* 126:1–13
- Borsje BW, de Vries MB, Bouma TJ, Besio G, Hulscher SJMH, Herman PMJ (2009) Modeling biogeomorphological influences for offshore sandwaves. *Cont Shelf Res* 29:1289–1301
- Braendle C, Heyland A, Flatt T (2011) Integrating mechanistic and evolutionary analysis of life history variation. In: Flatt T, Heyland A (eds) *Mechanisms of life history evolution. The genetics and physiology of life history traits and trade-offs*. Oxford University Press, New York, NY, p 3–10

- Bremner J, Rogers SI, Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Mar Ecol Prog Ser* 254:11–25
- Bremner J, Rogers SI, Frid CLJ (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst* 60:302–331
- Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? *Trends Ecol Evol* 32:429–437
- Cheng CH, Borsje BW, Beauchard O, O’Flynn S, Ysebaert T, Soetaert K (2021) Small scale microbenthic community structure along asymmetrical sand waves in an underwater seascape. *Mar Ecol* 42:e12657
- Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package - I - One-table methods. *R News* 4:5–10
- Cronin K (2012) Habitats on the NCP: model parameters. Trends in indicators of seabed integrity and evaluation of the impact of natural factors and human activities. *Deltares Rep* 1205122-000. Deltares, Delft
- Daan R, Mulder M (2009) Monitoring the invertebrate benthic fauna in the Dutch sector of the North Sea 1991–2005: an overview. *NIOZ Rep* 2009-5. NIOZ, Den Burg
- Dahl E (1952) Some aspects of the ecology and zonation of the fauna on sandy beaches. *Oikos* 4:1–27
- Damveld JH, van der Reijden KJ, Cheng C, Koop L and others (2018) Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. *Geophys Res Lett* 45:11837–11846
- Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol Lett* 15:1378–1386
- Darr D, Gogina M, Zettler ML (2014) Functional changes in benthic communities along a salinity gradient – a western Baltic case study. *J Sea Res* 85:315–324
- Diaz R, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–303
- Dray S, Legendre P (2008) Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89:3400–3412
- Dray S, Chessel D, Thioulouse J (2003) Co-inertia analysis and the linking of ecological data tables. *Ecology* 84:3078–3089
- Dray S, Dufour AB, Chessel D (2007) The ade4 Package - II: Two-table and K-table methods. *R News* 7:47–54
- Dray S, Péliissier R, Couteron P, Fortin MJ and others (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecol Monogr* 82:257–275
- Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95:14–21
- Dray S, Blanchet G, Borcard D, Clappe S and others (2018) adespatial: multivariate multiscale spatial analysis. R package version 02-0. <https://CRAN.R-project.org/package=adespatial>
- Duineveld GCA, de Wilde PAWJ, Kok A (1992) A synopsis of the macrobenthic assemblages and benthic ETS activity in the Dutch sector of the North Sea. *Neth J Sea Res* 28:125–138
- Dutch Ministry of Infrastructure and Water Management (2013) Rijkswaterstaat North Sea Directorate. www.noordzeeloket.nl
- EMODnet Bathymetry Consortium (2018) EMODnet digital bathymetry (DTM 2018). <https://doi.org/10.12770/18ff0d48-b203-4a65-94a9-5fd8b0ec35f6>
- Erdey-Heydorn MD (2008) An ArcGIS seabed characterization toolbox developed for investigating benthic habitats. *Mar Geod* 31:318–358
- Escoufier B, Pagès J (1990) Analyses factorielles simples et multiples: objectifs, méthodes et interprétation. Dunod, Paris
- Fleddum A, Atkinson LJ, Field JG, Shin P (2013) Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa. *J Mar Biol Assoc UK* 93:2027–2038
- Gerasimova AV, Maximovich NV (2013) Age–size structure of common bivalve mollusc populations in the White Sea: the causes of instability. *Hydrobiologia* 706:119–137
- Giangrande A, Geraci S, Belmonte G (1994) Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanogr Mar Biol Annu Rev* 32:305–333

- Gladstone-Gallagher RV, Hewitt JE, Thrush SF, Brustolin MC, Villnäs A, Valanko S, Norkko A (2021) Identifying ‘vital attributes’ for assessing disturbance–recovery potential of seafloor communities. *Ecol Evol* 11:6091–6103
- Grant J (1980) A flume study on drift in marine infaunal amphipods (Haustoriidae). *Mar Biol* 56:79–84
- Grassle JF, Grassle JP (1974) Opportunistic life histories and genetic systems in marine benthic polychaetes. *J Mar Res* 32:253–284
- Greenslade PJM (1983) Adversity selection and the habitat templet. *Am Nat* 122:352–365
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Grime JP, Pierce S (2012) *The evolutionary strategies that shape ecosystems*. Wiley-Blackwell, Chichester
- Günther CP (1992) Dispersal of intertidal invertebrates: a strategy to react to disturbance of different scales? *Neth J Sea Res* 30:45–56
- Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr Mar Biol Annu Rev* 32:179–239
- Harris PT, Baker EK (eds) (2020) *Seafloor geomorphology as benthic habitat*. GeoHab atlas of seafloor geomorphic features and benthic habitats, 2nd edn. Elsevier, Amsterdam
- Hewitt JE, Thrush SF, Dayton PD (2008) Habitat variation, species diversity and ecological functioning in a marine system. *J Exp Mar Biol Ecol* 366:116–122
- Hill MO, Smith AJE (1976) Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* 25:249–255
- Holzhauser H, Borsje BW, van Dalen JA, Wijnberg KM, Hulscher SJMH, Herman PMJ (2020) Benthic species distribution linked to morphological features of a barred coast. *J Mar Sci Eng* 8:16
- Huntley DA, Huthnance JM, Collins MB, Liu CL, Nicholls RJ, Hewitson C (1993) Hydrodynamics and sediment dynamics of North Sea sand waves and sand banks. *Philos Trans R Soc A* 343:461–474
- Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. *J Veg Sci* 3:157–164
- Kenny AJ, Jenkins C, Wood D, Bolam SG, Mitchell P, Scougal C, Judd A (2018) Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. *ICES J Mar Sci* 75:1080–1092
- Kindsater HK, Mangel M, Reynolds JD, Dulvy NK (2016) Ten principles from evolutionary ecology essential for effective marine conservation. *Ecol Evol* 6:2125–2138
- Kostylev VE, Hannah CG (2007) Process-driven characterization and mapping of seabed habitats. In: Todd BJ, Greene HG (eds) *Mapping the seafloor for habitat characterization*: Geological Association of Canada, Special Paper 47. Geological Association of Canada, St. John’s, p 171–184
- Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Mar Ecol Prog Ser* 446:285–302
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305
- Laliberté E, Legendre P, Shipley B (2014) FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. <https://cran.r-project.org/web/packages/FD/index.html>
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556
- Levin LA (1984) Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65:1185–1200
- Lundblad E, Wright DJ, Miller J, Larkin EM and others (2006) A benthic terrain classification scheme for American Samoa. *Mar Geod* 29:89–111
- Lytle DA (2001) Disturbance regimes and life-history evolution. *Am Nat* 157:525–536
- MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am Nat* 101:377–385
- McCall PL (1977) Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J Mar Res* 35:221–266

- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185
- Michailidis G, de Leeuw J (1998) The Gifi system of descriptive multivariate analysis. *Stat Sci* 13:307–336
- Murtagh F, Legendre P (2014) Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? *J Classif* 31:274–295
- Nilsson HC, Rosenberg R (2000) Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Mar Ecol Prog Ser* 197:139–149
- Nishisato S (2006) Correlation structure of multiple choice data as viewed from dual scaling. In: Greenacre M, Blasius J (eds) *Multiple correspondence analysis and related methods*. Chapman & Hall/CRC, London, p 161–177
- Norkko A, Rosenberg R, Thrush SF, Whitlatch RB (2006) Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. *J Exp Mar Biol Ecol* 330:195–207
- Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Mar Ecol Prog Ser* 332:11–23
- Oliver JS, Slattey PN, Hulberg LW, Nybakken JW (1980) Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fish Bull* 78:437–454
- Oug E, Fleddum A, Rygg B, Olsgard F (2012) Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. *J Exp Mar Biol Ecol* 432–433:94–105
- Pearson TH (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr Mar Biol Annu Rev* 39:233–267
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Annu Rev* 16:229–311
- Pechenik JA (1990) Delayed metamorphosis by larvae of benthic marine invertebrates: Does it occur? Is there a price to pay? *Ophelia* 32:63–94
- Peres-Neto PR, Leibold MA, Dray S (2012) Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. *Ecology* 93:S14–S30
- Peres-Neto PR, Dray S, ter Braak CJF (2017) Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography* 40:806–816
- Pianka ER (1970) On r- and K-selection. *Am Nat* 104:592–597
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ramirez Llodra E (2002) Fecundity and life history strategies in marine invertebrates. *Adv Mar Biol* 43:87–170
- Reise K (1982) Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? *Neth J Sea Res* 16:29–36
- Rijkswaterstaat (2013) Sediment map of the Dutch sector of the North Sea. Dutch Ministry of Infrastructure and Water Management. www.noordzeeloket.nl
- Rijkswaterstaat (2019) Directorate-General for Public Works and Water Management of the Dutch Ministry of Infrastructure and Water Management, Waterinfo Extra. <https://waterinfo-extra.rws.nl>
- Rhoads DC (1974) Organism–sediment relations on the muddy sea floor. *Oceanogr Mar* 12:263–300
- Rhoads DC, Germano JD (1982) Characterization of organism–sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remots™ System). *Mar Ecol Prog Ser* 8:115–128
- Rhoads DC, McCall PL, Yingst JY (1978) Disturbance and production on the estuarine seafloor. *Am Sci* 66:577–586
- Ridgway ID, Richardson CA (2011) *Arctica islandica*: the longest lived non colonial animal known to science. *Rev Fish Biol Fish* 21:297–310

- Robert P, Escoufier Y (1976) A unifying tool for linear multivariate statistical methods: the RV coefficient. *J R Stat Soc Ser C Appl Stat* 25:257–265
- Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia* 223:189–227
- Sameoto DD (1969) Some aspects of the ecology and life cycle of three species of subtidal sand-burrowing amphipods (Crustacea: Haustoriidae). *J Fish Res Board Can* 26:1321–1345
- Sanders HL (1968) Marine benthic diversity: a comparative study. *Am Nat* 102:243–282
- Santos SL, Simon JL (1980) Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. *Mar Ecol Prog Ser* 3:347–355
- Sepúlveda RD, Valdivia N (2017) Macrobenthic community changes of intertidal sandy shores after a mega-disturbance. *Estuaries Coasts* 40:493–501
- Snelgrove PVR (1999) Getting to the bottom of marine biodiversity: sedimentary habitats. *Bioscience* 49:129–138
- Snelgrove PVR, Butman CA (1994) Animal–sediment relationships revisited: cause versus effect. *Oceanogr Mar Biol Annu Rev* 32:111–177
- Solan M, Bradley J, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Evol Syst* 15:353–391
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *J Anim Ecol* 46:337–365
- Southwood TRE (1988) Tactics, strategies and templets. *Oikos* 52:3–18
- Stearns S (1992) *The evolution of life histories*. Oxford University Press, New York, NY
- Tenenhaus M, Young FW (1985) An analysis and synthesis of multiple correspondence analysis, optimal scaling, dual scaling, homogeneity analysis and other methods for quantifying categorical multivariate data. *Psychometrika* 50:91–119
- ter Braak CJF, Cormont A, Dray S (2012) Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology* 93:1525–1526
- Thakur MP, Wright AJ (2017) Environmental filtering, niche construction, and trait variability: the missing discussion. *Trends Ecol Evol* 32:884–886
- Thistle D, Yingst JY, Fauchald K (1985) A deep-sea benthic community exposed to strong near-bottom currents on the Scotian Rise (western Atlantic). *Mar Geol* 66:91–112
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45
- Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecol Appl* 22:2221–2236
- van Leeuwen S, Tett P, Mills D, van der Molen J (2015) Stratified and nonstratified areas in the North Sea: long-term variability and biological and policy implications. *J Geophys Res Oceans* 120:4670–4686
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301
- Villnäs A, Hewitt J, Snickars M, Westerbom M, Norkko A (2018) Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality. *Ecol Appl* 28:78–94
- Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74:159–164
- Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implication for population regulation. *Can J Fish Aquat Sci* 49:2196–2218
- Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER (2015) Functional traits, convergent evolution, and periodic tables of niches. *Ecol Lett* 18:737–751

Table S1. Detailed information on abiotic descriptors

Descriptor	Modality for qualitative descriptor	Detailed information	
Depth	Very shallow	< 10	Water depth in meters
	Shallow	[10; 20[
	Intermediate	[20; 30[
	Deep	[30; 40[
	Very deep	≥ 40	
Current speed	Very low	< 0.15	Monthly median value in meters per second averaged from 1996 to 2008
	Low	[0.15; 0.20[
	Intermediate	[0.20; 0.25[
	High	[0.25; 0.30[
	Very high	≥ 0.30	
Wave energy	Very low	< 0.5	Monthly median value in pascals averaged from 1996 to 2008
	Low	[0.5; 1.0[
	Intermediate	[1.0; 1.5[
	High	[1.5; 2.0[
	Very high	≥ 2.0	
Stratification	PM	Permanently mixed	Modeled hindcast results from 1958 to 2008
	FI	Freshwater influence	
	IS	Intermittently stratified	
	SS	Seasonally stratified	
	TR	Transitional	
Sediment type	Muddy	Includes: – Mud – Sandy mud – Sandy and slightly gravely mud – Muddy sand	
	Sandy	Sand	
	Coarse	Includes: – Gravel and muddy sand – Slightly gravely sand – Gravely sand – Sandy gravel – Gravel and stone	
	Mixed	Gravely and slightly muddy sand	
	Primary productivity		
Particulate organic matter		Percentages of dry sediment mass averaged from 1998 to 2008	
Particulate organic carbon			

Table S2. Detailed information on the biological trait data. “Code” indicates the corresponding trait modality in Table S3.

Trait	Modality	Code	Functional expression	Trait	Modality	Code	Functional expression
Body mass (classes mg AFWD)	Very small (<0.34)	1	Translates metabolic requirements and demands	Fertilization	Broadcasting	1	Possible in solitary dwelling species
	Small (0.34–2.60)	2			Spermcasting	2	Possible in relatively distant adults
	Medium (2.60–17.00)	3			Pairing	3	Necessary proximity between adults
	Large (17.00–150)	4		Offspring type	Egg	1	Offspring once released and
	Very large (>150.00)	5			Larva	2	independent from the parents
Motility	Sessile	1	Translates foraging and survival potentials	Juvenile	3	Translates offspring survival	
	Tubicolous	2		Offspring Size (mm)	<0.1	1	Reproductive allocation per capita
	Crawler	3			0.1–0.5	2	
	Crawler–Swimmer	4			0.5–1.5	3	
Burrowing depth	Surficial (or intermitently burried)	1	Deepest reachable sediment layer that enables to escape from predation or disturbance	>1.5	4	Offspring protection	
	Intermediate (0–5 cm)	2		None	1		
	Deep (5–15 cm)	3		Jelly mass	2		Expresses parental cares and offspring survival
	Very deep (>15 cm)	4		Collar mass	3		
Feeding type	Deposit feeding (De)	1	Informs on the nature of environmental resource (e.g. size, location and origin)	Bearing/Brooding	4	Offspring development	
	Suspension-deposit feeding (SuDe)	2		Internal	1		
	Suspension feeding (Su)	3		Lecithotrophic	2		Informs on embryonic vulnerability and adult reproductive effort
	Carnivory-Scavenging (CaSc)	4		Planktotrophic	3		
	Omnivory (Om)	5		Mixed lecithotrophic	4		
Life span (years)	<1	1	Time necessary to achieve a life cycle during which at least one reproductive success is ensured	Mixed planktotrophic	5	Offspring benthic stage duration (days)	
	1–3	2		Null	1		
	3–10	3		1–15	2		Critical time on the sea floor necessary to achieve offspring development
	>10	4		>15	3		
Age at maturity (years) (years)	<1	1	Time after which reproductive success can be expected; informs also on growth rate	Offspring pelagic stage duration (days)	Null	1	Critical time in the water column necessary to achieve offspring development
	1–3	2			1–15	2	
	>3	3			>15	3	
Reproductive frequency	Seasonal	1	Degree of reproductive resilience				
	Continuous	2					
Annual fecundity (number of offspring)	<10 ²	1	Potential of annual demographic recruitment				
	10 ² –10 ³	2					
	10 ³ –10 ⁴	3					
	10 ⁴ –10 ⁵	4					
	>10 ⁵	5					

Table S3. Biological trait data. Body mass was derived from the field data as explained in the text. References are listed below the table

Taxon	Body mass	Motility	Burrowing depth	Feeding type	Life span	Age at maturity	Reproductive frequency	Annual fecundity	Fertilisation	Offspring type	Offspring size	Offspring protection	Offspring development	Offspring benthic stage duration	Offspring pelagic stage duration	References
<i>Abludomelita obtusata</i>	1	4	1	1	1	1	2	1	3	3	4	4	1	3	1	50,156,182,209,218,246,353,395,474
<i>Abra alba</i>	2	3	3	2	2	1	1	4	1	1	1	1	5	1	3	117,118,125,269,470
<i>Abra nitida</i>	2	3	2	2	2	1	2	2	1	1	1	1	5	1	3	60,125,182,294,476,477
<i>Abra prismatica</i>	3	3	2	2	2	2	1	4	1	1	1	1	5	1	3	117,125,294
<i>Abra tenuis</i>	1	3	2	2	2	2	1	2	2	1	2	2	4	3	1	125,130,193,234,269
<i>Acanthocardia</i> sp.	4	3	2	3	4	2	1	5	1	1	1	1	5	1	3	125,182,294,356,447
<i>Acrocnida brachiata</i>	4	3	3	3	3	3	1	4	3	1	2	1	5	1	2	52,53,171,187,291,294,320
<i>Acteon tornatilis</i>	2	3	3	4	2	2	1	5	3	1	1	3	3	3	3	125,179,496,497
<i>Alitta virens</i>	5	4	4	5	2	2	1	4	3	1	2	4	2	2	3	31,171,258,348,487
<i>Ampelisca brevicornis</i>	2	4	1	1	2	1	1	1	3	3	4	4	1	3	1	97,116,209,353
<i>Ampelisca macrocephala</i>	2	4	1	1	2	1	1	1	3	3	4	4	1	3	1	251,353
<i>Ampelisca spinipes</i>	1	4	1	1	2	1	1	1	3	3	4	4	1	3	1	209,246,251,294,295,353,384,394,492
<i>Ampelisca tenuicornis</i>	1	4	1	1	2	1	1	1	3	3	4	4	1	3	1	115,209,353,424,448,464
<i>Ampharete</i> sp.	2	2	3	1	1	1	1	3	3	1	2	1	4	2	1	45,118,189,294,371
<i>Amphipholis squamata</i>	1	3	1	5	2	2	2	1	3	3	4	4	1	3	1	143,151,248
<i>Amphiura chiajei</i>	3	3	3	1	4	3	1	4	3	1	2	1	5	1	3	61,164,230,294,319
<i>Amphiura filiformis</i>	3	3	2	2	4	3	1	4	3	1	1	1	5	1	3	51,54,61,142,314,321,464
<i>Aonides paucibranchiata</i>	1	3	2	1	1	1	1	2	2	1	2	1	4	1	2	41,163,182,294,375,484
<i>Aphelocheata marioni</i>	2	3	2	1	3	2	1	2	3	1	2	2	4	2	1	109,118,160,163,192,194,362
<i>Aphrodita aculeata</i>	5	3	2	4	3	2	1	5	1	1	1	1	4	1	2	71,171,182,294,475
<i>Aporrhais pespelecani</i>	5	3	1	1	3	2	1	3	3	1	2	3	3	2	3	125,196,273,295,358,415
<i>Arcopagia crassa</i>	2	3	3	2	3	2	1	4	1	1	1	1	5	1	3	125,182,446
<i>Arctica islandica</i>	4	1	2	2	4	3	1	5	1	1	1	1	5	1	3	67,125,284,316,383,445,467
<i>Asbjornsenia pygmaea</i>	2	3	2	3	3	2	1	3	1	1	1	1	5	1	3	125,182,294
<i>Astarte montagui</i>	3	3	1	3	3	2	1	3	1	1	2	1	4	1	3	125,396,418,427,467
<i>Asterias rubens</i>	5	3	1	4	3	2	1	5	1	1	2	1	5	1	3	26,49,171,466
<i>Astropecten irregularis</i>	5	3	1	4	3	2	1	5	1	1	2	1	5	1	3	84,171,177,200,294,325
<i>Balanus crenatus</i>	1	1	1	3	2	1	1	3	3	2	2	4	3	3	3	27,28,171,353,373,376
<i>Bathyporeia elegans</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	168,169,209,246,327,353
<i>Bathyporeia gracilis</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	169,171,182,209,246,294,327,353
<i>Bathyporeia guilliamsoniana</i>	2	4	1	1	1	1	2	1	3	3	3	4	1	3	1	168,169,171,209,246,327,353
<i>Bathyporeia pelagica</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	168,169,209,327,353
<i>Bathyporeia sarsi</i>	1	4	1	1	1	1	2	1	3	3	4	4	1	3	1	171,182,246,294,327,353,465
<i>Bathyporeia tenuipes</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	169,171,209,246,294,327,353
<i>Bela nebula</i>	2	3	1	4	2	1	1	2	3	1	2	3	2	3	3	125,131,196,274
<i>Bodotria arenosa</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	182,246,249,353,423,493
<i>Bodotria scorpioides</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	246,249,353,423,493
<i>Branchiostoma lanceolatum</i>	3	4	2	3	3	2	1	3	1	1	2	1	5	1	3	136,180,228,270,385
<i>Brissopsis lyrifera</i>	5	3	2	1	3	3	1	5	1	1	1	1	5	1	3	63,64,166,229,434
<i>Buccinum undatum</i>	5	3	1	4	4	3	1	3	3	1	2	3	4	3	1	125,254,296
<i>Bylgides sarsi</i>	2	3	1	4	2	2	1	4	1	1	2	1	5	1	3	3,294,404
<i>Callianassa subterranea</i>	4	3	4	1	2	2	1	3	3	2	4	4	3	3	3	231,260,353,388,389,390
<i>Capitella capitata</i>	1	2	2	1	1	1	2	2	3	2	2	4	2	2	2	4,44,176,231,306

Table S3. Continued

Taxon	Body mass	Motility	Burrowing depth	Feeding type	Life span	Age at maturity	Reproductive frequency	Annual fecundity	Fertilisation	Offspring type	Offspring size	Offspring protection	Offspring development	Offspring benthic stage duration	Offspring pelagic stage duration	References
<i>Carcinus maenas</i>	5	3	1	5	3	2	1	5	3	2	4	4	3	3	3	34,101,171,308,353,469
<i>Chaetopterus variopedatus</i>	5	2	4	3	2	2	1	5	1	1	2	1	5	1	3	147,152,182,231,444,473
<i>Chaetozone setosa</i>	2	3	3	1	2	1	1	3	1	1	2	1	4	3	1	73,86,227,231,294,349
<i>Chamelea striatula</i>	3	3	2	3	4	2	1	5	1	1	1	1	5	1	3	15,125,133,210,231,488
<i>Cheirocratus sundevalli</i>	1	4	1	1	1	1	1	1	3	3	4	4	1	3	1	97,182,209,246,294,443,474
<i>Corbula gibba</i>	2	3	2	2	2	2	1	4	1	1	1	1	5	1	3	125,182,233,495
<i>Corophium</i> sp.	2	4	3	2	1	1	2	1	3	3	3	4	1	2	1	171,172,238,305,353
<i>Corystes cassivelaunus</i>	5	3	1	4	3	2	1	2	3	2	4	4	3	3	3	171,216,236,294,353
<i>Crangon crangon</i>	4	4	1	4	3	2	1	3	3	2	4	4	3	3	3	100,171,222,339,353,365,469
<i>Diastylis bradyi</i>	2	4	1	1	1	1	1	1	3	3	4	4	1	3	1	94,135,231,246,249,353,463
<i>Diastylis lucifera</i>	1	4	1	1	1	1	1	1	3	3	4	4	1	3	1	94,135,351,359
<i>Diastylis rathkei</i>	2	4	1	1	1	1	1	1	3	3	4	4	1	3	1	231,353,359,463
<i>Diogenes pugilator</i>	3	3	1	4	1	1	2	2	3	2	3	4	3	3	3	171,182,285,292,293,353,364,451
<i>Donax vittatus</i>	4	3	3	3	3	2	1	5	1	1	1	1	5	1	3	20,21,125,449
<i>Dosinia exoleta</i>	4	3	3	3	4	2	1	5	1	1	1	1	5	1	3	125,182,294,455,458
<i>Dosinia lupinus</i>	4	3	3	3	4	2	1	5	1	1	1	1	5	1	3	125,182,294,456
<i>Dyopedos monacanthus</i>	1	4	1	3	1	1	2	2	3	3	3	4	1	3	1	353,442
<i>Ebalia</i> sp.	4	3	1	5	2	2	1	3	3	2	3	4	3	3	3	246,271,294,397,408,409,410,411
<i>Echinocardium</i> sp.	4	3	3	1	4	3	1	5	1	1	2	1	5	1	3	62,79,123,124,212,231,309
<i>Echinocyamus pusillus</i>	2	3	2	1	2	2	1	4	1	1	2	1	5	1	3	171,188,231,280,294
<i>Ensis ensis</i>	5	3	3	3	4	3	1	5	1	1	1	1	5	1	3	125,171,223,294
<i>Ensis leei</i>	5	3	3	3	3	2	1	4	1	1	1	1	5	1	3	23,125,281,294
<i>Ensis magnus</i>	5	3	3	3	4	3	1	5	1	1	1	1	5	1	3	104,125,224
<i>Ensis siliqua</i>	5	3	3	3	4	3	1	5	1	1	1	1	5	1	3	105,125,158,223
<i>Eteone flava</i>	1	3	2	4	2	2	1	2	2	2	2	4	3	2	3	102,163,264,294,349
<i>Eteone longa</i>	2	3	2	4	2	2	1	2	3	1	2	1	5	1	3	231,294,350,377,378
<i>Eulalia</i> sp.	1	3	1	4	2	2	1	2	2	1	2	2	3	2	3	37,150,163,182,218,294,343,345
<i>Eumida sanguinea</i>	2	3	2	4	2	1	1	2	1	1	1	1	5	1	3	65,163,231,294,295
<i>Eunereis longissima</i>	4	3	1	5	1	1	1	4	1	1	2	1	4	1	2	163,182,294,435
<i>Eupolyommia nebulosa</i>	2	2	2	1	2	2	1	4	2	1	2	2	4	2	1	36,38,39,201,202,302,332
<i>Eurydice pulchra</i>	4	4	1	4	2	2	1	1	3	3	4	4	1	3	1	173,246,247,353
<i>Euspira catena</i>	5	3	1	4	3	2	1	3	3	1	2	3	4	2	1	18,19,125,196,197,275
<i>Euspira nitida</i>	3	3	1	4	3	2	1	4	3	1	2	3	2	3	3	17,125,255,256,275
<i>Fabulina fabula</i>	3	3	3	2	3	2	1	4	1	1	1	1	5	1	3	125,171,182,231,294,470
<i>Galathowenia oculata</i>	1	2	2	1	1	1	1	4	1	1	2	1	5	1	3	159,163,167,186,257,263,303
<i>Gammaropsis</i> sp.	1	4	1	1	2	1	1	1	3	3	4	4	1	3	1	209,239,246,294,322,353
<i>Gammarus</i> sp.	1	4	1	1	2	1	2	1	3	3	4	4	1	3	1	13,95,246,353
<i>Gari fervensis</i>	4	3	2	3	3	2	1	3	1	1	2	1	5	1	3	91,125,128,294,425
<i>Gastrosaccus spinifer</i>	2	4	1	5	2	1	2	1	3	3	4	4	1	2	1	171,289,294,353,378
<i>Gattyana cirrhosa</i>	4	3	4	4	3	2	1	4	1	1	2	1	5	1	3	102,182,231
<i>Gilvossius tyrrenus</i>	4	3	4	1	2	2	1	2	3	2	4	4	3	3	2	146,260,353,354,439,440
<i>Glycera</i> sp.	3	4	4	4	3	3	1	5	1	1	2	1	5	1	3	70,98,99,163,294,335,487
<i>Goniada maculata</i>	2	4	2	4	2	1	1	2	1	1	2	1	5	1	3	182,231,257,294,299
<i>Harmothoe</i> sp.	3	3	1	4	2	2	1	4	3	2	2	4	3	2	3	102,110,163,171,231,294,378
<i>Harpinia antennaria</i>	1	4	1	5	1	1	2	1	3	3	4	4	1	3	1	209,231,246,353,391,395,474
<i>Haustorius arenarius</i>	1	4	3	2	1	1	1	1	3	3	4	4	1	3	1	134,138,182,353,461

Table S3. Continued

Taxon	Body mass	Motility	Burrowing depth	Feeding type	Life span	Age at maturity	Reproductive frequency	Annual fecundity	Fertilisation	Offspring type	Offspring size	Offspring protection	Offspring development	Offspring benthic stage duration	Offspring pelagic stage duration	References
<i>Hediste diversicolor</i>	5	4	4	5	2	2	1	3	3	2	2	4	2	2	3	108,140,154,171,189,203,407
<i>Heteromastus filiformis</i>	2	2	4	1	2	2	1	2	3	1	2	2	3	2	3	40,198,422
<i>Hiatella arctica</i>	3	1	1	3	4	2	1	1	1	1	1	1	4	1	3	56,125,294,417
<i>Hypereteone foliosa</i>	3	3	3	4	2	1	1	3	1	1	2	1	5	1	3	163,182,294,349,486
<i>Idotea linearis</i>	1	4	1	5	2	1	2	2	3	3	4	4	1	3	1	171,175,353
<i>Iphinoe trispinosa</i>	2	4	1	1	1	1	2	1	3	3	3	4	1	3	1	93,353,423
<i>Jassa marmorata</i>	1	4	1	3	1	1	2	1	3	3	3	4	1	2	1	88,323,353,395,414
<i>Kellia suborbicularis</i>	3	3	2	1	2	2	1	2	2	2	1	4	3	2	3	125,277,342
<i>Kurtiella bidentata</i>	1	3	2	1	2	2	1	2	2	2	2	4	3	3	3	125,334
<i>Lagis koreni</i>	3	2	3	1	2	2	1	4	1	1	1	1	5	1	2	118,231,237,265,326,441
<i>Lanice conchilega</i>	3	2	3	2	2	1	1	4	1	1	2	1	5	1	3	36,171,189,258,294,374
<i>Laonice</i> sp.	2	2	4	1	2	1	1	2	2	1	2	1	5	1	3	41,46,163,294,426,484
<i>Lepidonotus squamatus</i>	3	3	1	5	3	1	1	2	1	1	1	1	5	1	3	163,263,294,369,378
<i>Leptosynapta inhaerens</i>	4	3	3	1	3	2	1	2	3	3	4	4	1	2	1	171,294,419,420
<i>Limecola balthica</i>	3	3	3	2	3	2	1	5	1	1	2	1	5	1	3	125,204,232,266,283,340
<i>Liocarcinus</i> sp.	5	4	1	4	3	2	1	4	3	2	4	4	3	3	3	1,2,25,57,81,82,83,87,165,171,173,178,182,217,294,318,353
<i>Lucinoma borealis</i>	4	3	4	3	3	2	1	3	1	1	2	1	4	1	3	111,125,206,457
<i>Lumbrineris</i> sp.	3	3	3	5	3	3	1	3	2	1	2	2	4	3	1	163,231,294,328,361,406
<i>Lutraria lutraria</i>	5	3	4	3	4	3	1	5	1	1	1	1	5	1	3	125,182,240,253
<i>Macomangulus tenuis</i>	3	3	2	2	3	2	1	4	1	1	1	1	5	1	3	22,30,125,129,182,432,452
<i>Maetra stultorum</i>	4	3	3	3	3	2	1	5	1	1	1	1	5	1	3	74,80,125,182
<i>Magelona</i> sp.	2	3	3	2	2	1	1	3	1	1	2	1	5	1	3	163,182,214,294,295,315,380,483
<i>Malacoceros fuliginosus</i>	4	4	2	2	2	2	1	3	2	1	2	1	5	1	3	41,46,121,122,163,171,207,294
<i>Malmgrenia lunulata</i>	2	3	3	4	3	2	1	5	1	1	1	1	5	1	3	163,182,231,294,295,502
<i>Mediomastus fragilis</i>	2	2	2	1	2	1	1	2	1	1	2	2	3	2	3	163,182,215,294,378
<i>Megaluropus agilis</i>	1	4	1	1	1	1	2	1	3	3	2	4	1	3	1	155,168,182,209,246,353
<i>Mesopodopsis slabberi</i>	2	4	1	5	1	1	2	1	3	3	4	4	1	2	1	132,171,353,381,472
<i>Mimachlamys varia</i>	3	1	1	3	3	2	1	5	1	1	1	1	5	1	3	55,125,294,379,421
<i>Modiolus</i> sp.	4	1	1	3	4	3	2	5	1	1	1	1	5	1	3	125,126,294,416
<i>Musculus</i> sp.	3	1	1	2	3	2	1	2	2	3	3	4	4	3	1	125,286,307,336
<i>Mya arenaria</i>	5	1	4	3	4	3	1	5	1	1	1	1	5	1	3	58,59,125,433
<i>Mya truncata</i>	5	1	3	3	4	3	1	5	1	1	1	1	5	1	3	8,9,56,125,182,294
<i>Mysia undata</i>	3	3	3	3	2	2	1	4	1	1	1	1	5	1	3	16,125,182,298
<i>Mytilus edulis</i>	3	1	1	3	4	2	1	5	1	1	1	1	5	1	3	125,127,235,294
<i>Nassarius reticulatus</i>	5	3	1	4	3	3	1	3	3	1	2	3	3	3	3	77,125,171,272,436
<i>Natatolana borealis</i>	3	4	3	4	3	2	2	1	3	3	4	4	1	3	1	244,250,290,438,490
<i>Nephrops norvegicus</i>	5	3	4	4	3	3	1	3	3	2	4	4	3	3	3	161,162,226,304,313,353,401,454
<i>Nephtys</i> sp.	3	4	4	4	3	2	1	4	1	1	2	1	5	1	3	68,69,89,137,182,189,231,257,264,294,297,344,346,347,413,453,484,500,501
<i>Notomastus latericeus</i>	4	3	4	1	1	1	1	2	1	1	2	1	4	1	2	163,190,294,478,481,484
<i>Nucula nitidosa</i>	2	3	2	1	3	2	1	3	1	1	2	1	4	1	2	118,119,125,294,380,485
<i>Nucula nucleus</i>	2	3	3	1	3	2	1	2	1	1	2	1	4	1	2	125,294
<i>Ophelia</i> sp.	3	3	2	1	2	2	1	2	1	1	2	1	4	1	2	163,257,294,372,482
<i>Ophiura</i> sp.	3	4	1	5	3	2	1	3	1	1	2	1	5	1	3	48,106,171,294,460
<i>Owenia fusiformis</i>	3	2	3	1	2	2	1	4	1	1	2	1	5	1	3	10,102,107,118,171,186,329,480
<i>Oxydromus flexuosus</i>	3	4	2	4	2	2	1	4	1	1	2	1	5	1	3	211,352

Table S3. Continued

Taxon	Body mass	Motility	Burrowing depth	Feeding type	Life span	Age at maturity	Reproductive frequency	Annual fecundity	Fertilisation	Offspring type	Offspring size	Offspring protection	Offspring development	Offspring benthic stage duration	Offspring pelagic stage duration	References
<i>Pagurus bernhardus</i>	5	3	1	4	3	2	1	4	3	2	4	4	3	3	3	120,148,171,267,268
<i>Paraonis fulgens</i>	2	3	3	1	1	1	1	2	1	1	2	1	4	3	1	35,153,182,185,294,378,386,491
<i>Peringia ulvae</i>	1	3	1	1	2	1	1	2	3	1	2	3	2	3	3	11,29,125,170,171,428
<i>Pericolodes longimanus</i>	1	4	4	5	1	1	2	1	3	3	4	4	1	3	1	32,231,245,324,353
<i>Petricolaria pholadiformis</i>	5	3	3	3	3	3	1	5	1	1	1	1	5	1	3	6,125,145,392
<i>Phaxas pellucidus</i>	3	3	2	3	3	2	1	4	1	1	1	1	5	1	3	125,182,276
<i>Philocheras trispinosus</i>	4	4	1	4	1	1	2	2	3	2	4	4	3	2	3	262,337,338,353,360,400
<i>Pholoe minuta</i>	2	3	1	4	3	3	1	4	1	1	2	1	5	1	3	85,125,219,220,221,368
<i>Phoronis</i> sp.	2	2	3	3	1	1	2	2	1	1	1	1	5	1	3	41,149,205
<i>Photis longicaudata</i>	1	4	1	1	1	1	2	1	3	3	2	4	1	3	1	182,209,246,310,353,395,479
<i>Phyllodoce</i> sp.	3	3	3	4	3	2	1	4	3	1	2	2	4	1	3	231,279,317,393
<i>Pisione remota</i>	1	3	1	4	2	2	1	2	3	1	1	1	3	2	3	5,144,163,189,294,431
<i>Poecilochaetus serpens</i>	2	2	2	2	1	1	1	2	1	1	2	1	5	1	3	163,182,189,294,295,331
<i>Polydora</i> sp.	2	2	2	2	1	1	1	2	2	2	2	4	3	2	3	14,41,112,171,207,287,499
<i>Pontocrates altamarinus</i>	1	4	1	5	2	1	1	1	3	3	4	4	1	3	1	32,209,231,246,353
<i>Pontocrates arcticus</i>	1	4	1	5	1	1	2	1	3	3	4	4	1	3	1	32,33,209,246,353
<i>Pontocrates arenarius</i>	1	4	1	5	2	1	2	1	3	3	4	4	1	3	1	32,168,209,246,353,468
<i>Portunus latipes</i>	3	4	1	5	2	1	1	4	3	2	4	4	3	3	3	76,92,245,278,353,355
<i>Prionospio</i> sp.	1	2	2	2	1	1	1	2	2	1	2	1	5	1	3	41,294,330,484
<i>Pseudocuma longicornis</i>	1	4	1	1	1	1	2	1	3	3	3	4	1	3	1	93,231,294,353,423
<i>Pygospio elegans</i>	1	2	2	5	2	1	1	2	2	2	2	4	3	3	3	14,41,46,207,301,312,363
<i>Scalibregma inflatum</i>	2	3	4	1	1	1	1	2	1	1	2	1	4	1	2	139,163,288,294
<i>Schistomysis</i> sp.	2	4	1	5	1	1	2	1	3	3	4	4	1	2	1	171,218,246,294,300,353,398,399,489
<i>Scolelepis squamata</i>	3	4	4	2	2	2	1	3	1	1	2	1	5	1	3	46,113,231,382,429
<i>Scoletoma fragilis</i>	2	3	3	4	3	3	1	2	1	1	2	2	4	3	1	163,218,294,349,405,462
<i>Scoloplos armiger</i>	3	3	3	1	2	2	1	3	1	1	2	1	4	2	1	12,75,191,231,259,367,412
<i>Sigalion mathildae</i>	3	3	4	4	3	3	1	4	1	1	2	1	5	1	3	182,189,231,303
<i>Sphenia binghami</i>	2	1	1	3	4	3	1	4	1	1	1	1	5	1	3	125,182,213,294,494
<i>Spio decoratus</i>	1	2	2	1	1	1	1	3	2	2	2	4	2	2	2	41,163,189,195,208
<i>Spio filicornis</i>	2	2	2	1	1	1	2	2	2	2	3	4	3	2	2	41,195,231,430,437
<i>Spio martinensis</i>	2	2	2	1	1	1	2	3	2	2	2	4	2	2	2	41,46,163,207,208,294,437
<i>Spiophanes bombyx</i>	2	2	2	2	2	1	1	2	2	1	2	1	5	1	3	41,46,103,114,231,294,380,484
<i>Spirobranchus triqueter</i>	1	2	1	3	2	1	2	2	1	1	1	1	5	1	3	96,163,171,261
<i>Spisula elliptica</i>	3	3	2	3	3	2	1	5	1	1	1	1	5	1	3	125,182,294
<i>Spisula solida</i>	4	3	2	3	4	3	1	5	1	1	1	1	5	1	3	125,157,171,242,243
<i>Spisula subtruncata</i>	4	3	2	3	3	2	1	5	1	1	1	1	5	1	3	66,118,125
<i>Streblospio shrubsolii</i>	1	2	2	2	1	1	2	1	2	3	3	4	4	2	1	41,46,72,387,402
<i>Streptosyllis websteri</i>	1	3	2	1	3	3	1	3	3	1	2	1	4	1	3	163,174,184,303
<i>Synchelidium maculatum</i>	1	4	1	5	1	1	1	1	3	3	4	4	1	3	1	32,209,246,353,468,498
<i>Tellimyia ferruginosa</i>	2	3	3	3	2	1	1	2	2	2	1	4	3	3	3	125,171,181,231,277,341,342
<i>Terebellides stroemii</i>	3	2	3	1	2	1	1	3	2	1	2	2	4	2	1	102,141,163,183
<i>Tharyx</i> sp.	1	3	2	1	2	2	1	3	1	1	2	1	4	2	1	47,109,118,160,163,362
<i>Thelepus cincinnatus</i>	2	2	2	1	1	1	1	4	2	2	2	4	4	2	1	163,182,241,302
<i>Thracia convexa</i>	4	3	3	3	3	2	1	3	2	2	2	4	4	3	1	7,78,125,294,403
<i>Thracia phaseolina</i>	3	3	4	3	4	2	1	3	2	2	2	4	4	3	1	7,125,294,403
<i>Thracia pubescens</i>	5	3	3	3	4	2	1	3	2	2	2	4	4	3	1	7,125,294,333,403

Table S3. Continued

Taxon	Body mass	Motility	Burrowing depth	Feeding type	Life span	Age at maturity	Reproductive frequency	Annual fecundity	Fertilisation	Offspring type	Offspring size	Offspring protection	Offspring development	Offspring benthic stage duration	Offspring pelagic stage duration	References
<i>Thyasira flexuosa</i>	2	3	3	3	3	2	1	2	2	1	2	3	4	3	1	42,43,118,125,199,225,282
<i>Tryphosa nana</i>	1	4	1	4	1	1	2	1	3	3	3	4	1	3	1	311
<i>Turritellinella tricarinata</i>	4	3	2	3	3	2	1	3	3	1	1	3	3	2	2	125,252,273,295
<i>Upogebia deltaura</i>	5	3	4	2	3	2	1	3	3	2	4	4	3	3	3	294,353,366,459,471
<i>Urothoe brevicornis</i>	2	4	3	1	2	1	2	2	3	3	4	4	1	3	1	65,90,168,231,294,353,395
<i>Urothoe marina</i>	1	4	3	1	2	1	2	1	3	3	4	4	1	3	1	65,90,231,294,353
<i>Urothoe poseidonis</i>	1	4	3	1	2	1	2	2	3	3	4	4	1	3	1	65,90,231,294,353
<i>Venerupis corrugata</i>	5	1	3	3	3	2	1	5	1	1	1	1	5	1	3	125,243
<i>Venus</i> sp.	4	3	2	3	4	3	1	5	1	1	1	1	4	1	3	24,125,170,182,294,357,370,450
<i>Westwoodilla caecula</i>	1	4	1	1	1	1	2	1	3	3	4	4	1	3	1	33,246,353

REFERENCES

- Abelló P (1989) Reproduction and moulting in *Liocarcinus depurator* (Linnaeus, 1758) (Brachyura: Portunidae) in the Northwestern Mediterranean sea. *Sci Mar* 53:127–134
- Abelló P, Reid DG, Naylor E (1991) Comparative locomotor activity patterns in the portunid crabs *Liocarcinus holzatus* and *L. depurator*. *J Mar Biol Assoc UK* 71:1–10 [doi:10.1017/S0025315400037346](https://doi.org/10.1017/S0025315400037346)
- Abrams PA, Hill C, Elmgren R (1990) The functional response of the predatory polychaete, *Harmothoe sarsi*, to the amphipod, *Pontoporeia affinis*. *Oikos* 59:261–269 [doi:10.2307/3545543](https://doi.org/10.2307/3545543)
- Adkins M, Schulze A (2011) Development of *Capitella* sp. G from Galveston Bay, Texas. *Mar Biol Res* 7:202–207 [doi:10.1080/17451000.2010.489612](https://doi.org/10.1080/17451000.2010.489612)
- Åkesson B (1961) On the histological differentiation of the larvae of *Pisone remota* (Pisionidae, Polychaeta). *Acta Zoologica* 42:177–225 [doi:10.1111/j.1463-6395.1961.tb00063.x](https://doi.org/10.1111/j.1463-6395.1961.tb00063.x)
- Alexander RR, Stanton RJ Jr, Dodd JR (1993) Influence of sediment grain size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of Selected Neogene clams. *Palaios* 8:289–303 [doi:10.2307/3515151](https://doi.org/10.2307/3515151)
- Allen JA (1961) The British species of *Thracia* (Eulamellibranchia). *J Mar Biol Assoc UK* 41:723–735 [doi:10.1017/S0025315400016271](https://doi.org/10.1017/S0025315400016271)
- Amaro T, Duineveld G, Bergman M, Witbaard R (2003) Growth variations in the bivalve *Mya truncata*: a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? *Helgol Mar Res* 57:132–138 [doi:10.1007/s10152-003-0150-6](https://doi.org/10.1007/s10152-003-0150-6)
- Amaro T, Duineveld G, Tyler P (2005) Does *Mya truncata* reproduce at its southern distribution limit? *J Shellfish Res* 24:25–28 [doi:10.2983/0730-8000\(2005\)24\[25:DMTRAI\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2005)24[25:DMTRAI]2.0.CO;2)
- Ambrogi R, Fontana P, Gambi MC 1995. Population dynamics and estimate of secondary production of *Owenia fusiformis* Delle Chiaje (Polychaeta, Oweniidae) in the coastal area of the Po River Delta (Italy). In: Eleftheriou, A. et al. (editor.) (1995). *Biology and ecology of shallow coastal waters. Proceedings of the 28th European Marine Biological Symposium, Crete, Greece, 23-28 September 1993. International Symposium Series*, pp 207–214.
- Anderson DT (1959) The embryology of the polychaete *Scoloplos armiger*. *J Cell Sci* s3-100:89–166 [doi:10.1242/jcs.s3-100.49.89](https://doi.org/10.1242/jcs.s3-100.49.89)

11. Anderson A (1971) Intertidal activity, breeding and the floating habit of *Hydrobia ulvae* in the Ythan estuary. *J Mar Biol Assoc UK* 51:423–437 [doi:10.1017/S0025315400031891](https://doi.org/10.1017/S0025315400031891)
13. Andersson S, Persson M, Moksnes PO, Baden S (2009) The role of the amphipod *Gammarus locusta* as a grazer on macroalgae in Swedish seagrass meadows. *Mar Biol* 156:969–981 [doi:10.1007/s00227-009-1141-1](https://doi.org/10.1007/s00227-009-1141-1)
14. Anger K, Anger V, Hagmeier E (1986) Laboratory studies on larval growth of *Polydora ligni*, *Polydora ciliata*, and *Pygospio elegans* (Polychaeta, Spionidae). *Helgol Meeresunters* 40:377–395 [doi:10.1007/BF01983819](https://doi.org/10.1007/BF01983819)
15. Ansell AD (1961) Reproduction, growth and mortality of *Venus striatula* (Da Costa) in Kames Bay, Millport. *J Mar Biol Assoc UK* 41:191–215 [doi:10.1017/S0025315400001648](https://doi.org/10.1017/S0025315400001648)
16. Ansell AD (1961) The functional morphology of the British species of Veneracea (Eulamellibranchia). *J Mar Biol Assoc UK* 41:489–517 [doi:10.1017/S0025315400024012](https://doi.org/10.1017/S0025315400024012)
17. Ansell AD (1981) Experimental studies of a benthic predator-prey relationship. I. Feeding, growth, and egg-collar production in long-term cultures of the gastropod drill *Polinices alderi* (Forbes) feeding on the bivalve *Tellina tenuis* (da Costa). *J Exp Mar Biol Ecol* 56:235–255 [doi:10.1016/0022-0981\(81\)90192-1](https://doi.org/10.1016/0022-0981(81)90192-1)
18. Ansell AD (1982) Experimental studies of a benthic predator-prey relationship: III. Factors affecting rate of predation and growth in juveniles of the gastropod drill, *Polinices catena* (da Costa) in laboratory cultures. *Malacologia* 22:367–375
19. Ansell AD (1983) Prey selection by the naticid gastropod, *Polinices catena*. *J Molluscan Stud* 49:1
20. Ansell AD (1983) The biology of the genus *Donax*. *Developments in Hydrobiology* 19:607–635
21. Ansell AD, Bodoy A 1979. Comparison of Events in the Seasonal Cycle for *Donax vittatus* and *D. trunculus* in European Waters. Cyclic Phenomena in Marine Plants and Animals. Proceedings of the 13th European Marine Biology Symposium, Isle of Man, 27 September–4 October 1978, pp 191–198.
22. Ansell AD, Trevallion A (1967) Studies on *Tellina tenuis* da costa I. Seasonal growth and biochemical cycle. *J Exp Mar Biol Ecol* 1:220–235 [doi:10.1016/0022-0981\(67\)90016-0](https://doi.org/10.1016/0022-0981(67)90016-0)
23. Armonies W, Reise K (1999) On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). *Helgol Mar Res* 52:291–300
24. Arneri E, Giannetti G, Antolini B (1998) Age determination and growth of *Venus verrucosa* L. (Bivalvia: Veneridae) in the southern Adriatic and the Aegean Sea. *Fish Res* 38:193–198 [doi:10.1016/S0165-7836\(98\)00146-5](https://doi.org/10.1016/S0165-7836(98)00146-5)
25. Aydın M, Karadurmuş U, Erbay M (2012) Length-weight relationships and reproduction characteristics of *Liocarcinus navigator* (Herbst, 1794). *Ege Journal of Fisheries and Aquatic Sciences* 29:193–197 [doi:10.12714/egejfas.2012.29.4.08](https://doi.org/10.12714/egejfas.2012.29.4.08)
26. Barker MF, Nichols D (1983) Reproduction, recruitment and juvenile ecology of the starfish, *Asterias rubens* and *Marthasterias glacialis*. *J Mar Biol Assoc UK* 63:745–765 [doi:10.1017/S0025315400071198](https://doi.org/10.1017/S0025315400071198)
29. Barnes RSK (1990) Reproductive strategies in contrasting populations of the coastal gastropod *Hydrobia ulvae*. II. Longevity and life-time egg production. *J Exp Mar Biol Ecol* 138:183–200 [doi:10.1016/0022-0981\(90\)90166-A](https://doi.org/10.1016/0022-0981(90)90166-A)
27. Barnes H, Barnes M (1954) The general biology of *Balanus balanus* (L.) Da Costa. *Oikos* 5:63–76 [doi:10.2307/3564651](https://doi.org/10.2307/3564651)
28. Barnes H, Barnes M (1968) Egg numbers, metabolic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. *J Exp Mar Biol Ecol* 2:135–153 [doi:10.1016/0022-0981\(68\)90004-X](https://doi.org/10.1016/0022-0981(68)90004-X)
30. Barnett PRO (1985) The effect of temperature on the growth of planktonic larvae of *Tellina tenuis* da Costa. *J Exp Mar Biol Ecol* 89:1–10 [doi:10.1016/0022-0981\(85\)90078-4](https://doi.org/10.1016/0022-0981(85)90078-4)
31. Bass NR, Brafield AE (1972) The life-cycle of the polychaete *Nereis Virens*. *J Mar Biol Assoc UK* 52:701–726 [doi:10.1017/S0025315400021664](https://doi.org/10.1017/S0025315400021664)

32. Beare DJ, Moore PG (1998) Aspects of the life histories of *Perioculodes longimanus*, *Pontocrates arcticus* and *Synchelidium maculatum* (Crustacea: Amphipoda) at Millport, Scotland. *J Mar Biol Assoc UK* 78:193–209 [doi:10.1017/S0025315400040029](https://doi.org/10.1017/S0025315400040029)
33. Beare DJ, Moore PG (1998) The life histories of offshore oedicerotids *Weswoodilla caecula* and *Monoculodes packardi* (Crustacea: Amphipoda) from Loch Fyne, Scotland. *J Mar Biol Assoc UK* 78:835–852 [doi:10.1017/S0025315400044829](https://doi.org/10.1017/S0025315400044829)
34. Berrill M (1982) The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *J Crustac Biol* 2:31–39 <https://doi.org/10.2307/1548108>
35. Bhaud M (1983) Premières observations de la larve planctonique récoltée en haute mer d'un représentant des Paraonidae (Annélide Polychète). *Vie Milieu* 33:41–48
36. Bhaud M (1988) The two planktonic larval periods of *Lanice conchilega* (Pallas, 1766) annelida polychaeta, a peculiar example of the irreversibility of evolution. *Ophelia* 29:141–152 [doi:10.1080/00785326.1988.10430825](https://doi.org/10.1080/00785326.1988.10430825)
39. Bhaud MR (1991) Larval release from the egg mass and settlement of *Eupolyornia nebulosa* (Polychaeta, Terebellidae). *Bull Mar Sci* 48:420–431
37. Bhaud M, Duchêne JC (1996) Change from planktonic to benthic development: is life cycle evolution an adaptive answer to the constraints of dispersal? *Oceanol Acta* 19:335–346
38. Bhaud M, Grémare A (1988) Larval development of terebellid polychaete *Eupolyornia nebulosa* (Montagu) in the Mediterranean Sea. *Zool Scr* 17:347–356 <https://doi.org/10.1111/j.1463-6409.1988.tb00111.x>
40. Bijkerk R, Dekker PI, Tydeman P 1996. Ecologisch profiel van de draadworm *Heteromastus filiformis* (Polychaeta). Rijksinstituut voor Kust en Zee, Rapport RIKZ 96-024, Den Haag, Nederlands, 72 p.
41. Bishop JDD, Pemberton AJ (2006) The third way: spermcast mating in sessile marine invertebrates. *Integr Comp Biol* 46:398–406 [PubMed doi:10.1093/icb/ijc037](https://pubmed.ncbi.nlm.nih.gov/doi/10.1093/icb/ijc037)
43. Blacknell WN 1973. Aspects of the biology of *Thyasira gouldi* (Philippi) and its copepod parasite *Axinophilus thyasirae* (Bresciani and Ockelmann). PhD thesis, University of Stirling, London, UK, 460 p.
42. Blacknell WM, Ansell AD (1974) The direct development of the bivalve *Thyasira gouldi* (Philippi). *Thalass Jugosl* 10:23–43
44. Blake JA (2009) Redescription of *Capitella capitata* (Fabricius) from West Greenland and designation of a neotype (Polychaeta, Capitellidae). *Zoosymposia* 2:55–80 [doi:10.11646/zoosymposia.2.1.7](https://doi.org/10.11646/zoosymposia.2.1.7)
45. Blake JA (2017) Larval development of Polychaeta from the northern California coast. Fourteen additional species together with seasonality of planktic larvae over a 5-year period. *J Mar Biol Assoc UK* 97:1081–1133 [doi:10.1017/S0025315417000716](https://doi.org/10.1017/S0025315417000716)
46. Blake JA, Arnofsky PL (1999) Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia* 402:57–106 [doi:10.1023/A:1003784324125](https://doi.org/10.1023/A:1003784324125)
47. Blake JA, Göransson P (2015) Redescription of *Tharyx killariensis* (Southern) from Ireland and description of two new species of *Tharyx* from the Kattegat, Sweden (Polychaeta, Cirratulidae). *Zootaxa* 4039:501–515 [PubMed doi:10.11646/zootaxa.4039.4.1](https://pubmed.ncbi.nlm.nih.gov/doi/10.11646/zootaxa.4039.4.1)
48. Boos K, Gutow L, Mundry R, Franke HD (2010) Sediment preference and burrowing behaviour in the sympatric brittlestars *Ophiura albida* Forbes, 1839 and *Ophiura ophiura* (Linnaeus, 1758) (Ophiuroidea, Echinodermata). *J Exp Mar Biol Ecol* 393:176–181 [doi:10.1016/j.jembe.2010.07.021](https://doi.org/10.1016/j.jembe.2010.07.021)
49. Borei H (1948) Respiration of oocytes, unfertilized eggs and fertilized eggs from *Psammechinus* and *Asterias*. *Biol Bull* 95:124–150 [PubMed doi:10.2307/1538159](https://pubmed.ncbi.nlm.nih.gov/doi/10.2307/1538159)
50. Bos OG, Witbaard R, Lavaleye M, van Moorsel G and others (2011) Biodiversity hotspots on the Dutch Continental Shelf. A Marine Strategy Framework Directive perspective. IMARES Wageningen UR, Report BO-11-011.04-009, 145 p.
51. Bourgoin A, Guillou M (1988) Démographie d'*Amphiura filiformis* (Echinodermata: Ophiuroidea) en baie de Concarneau (Finistère, France). *Oceanol Acta* 11:79–87

52. Bourgoin A, Guillou M (1990) Variations in the reproductive cycle of Acrocnida brachiata (Echinodermata: Ophiuroidea) according to environment in the Bay of Douarnenez (Brittany). *J Mar Biol Assoc UK* 70:57–66 [doi:10.1017/S0025315400034196](https://doi.org/10.1017/S0025315400034196)
53. Bourgoin A, Guillou M (1994) Arm regeneration in two populations of Acrocnida brachiata (Montagu) (Echinodermata: Ophiuroidea) in Douarnenez Bay, (Brittany: France): an ecological significance. *J Exp Mar Biol Ecol* 184:123–139 [doi:10.1016/0022-0981\(94\)90170-8](https://doi.org/10.1016/0022-0981(94)90170-8)
54. Bowner T (1982) Reproduction in *Amphiura filiformis* (Echinodermata: Ophiuroidea): seasonality in gonad development. *Mar Biol* 69:281–290 [doi:10.1007/BF00397493](https://doi.org/10.1007/BF00397493)
55. Brand AR 2006. The European scallop fisheries for *Pecten maximus*, *Aequipecten opercularis* and *Mimachlamys varia*. In: Shumway S.E., Parsons G.J. (editors). *Scallops: Biology, Ecology and Aquaculture*. Elsevier, pp 991–1058.
56. Brandner MM, Stübner E, Reed AJ, Gabrielsen TM, Thatje S (2017) Seasonality of bivalve larvae within a high Arctic fjord. *Polar Biol* 40:263–276 [doi:10.1007/s00300-016-1950-x](https://doi.org/10.1007/s00300-016-1950-x)
57. Bridges CR (1986) A comparative study of the respiratory properties and physiological function of haemocyanin in two burrowing and two non-burrowing crustaceans. *Comp Biochem Physiol Part A Physiol* 83:261–270 [doi:10.1016/0300-9629\(86\)90572-4](https://doi.org/10.1016/0300-9629(86)90572-4)
58. Brousseau DJ (1978) Spawning cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. *Fish Bull* 76:155–166
59. Brousseau DJ (1979) Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Mar Biol* 51:221–227 [doi:10.1007/BF00386801](https://doi.org/10.1007/BF00386801)
60. Brown RA (1982) Reproduction of *Abra nitida* (Müller) (Bivalvia) in the southern Skagerrak. *Sarsia* 67:55–60 [doi:10.1080/00364827.1982.10421332](https://doi.org/10.1080/00364827.1982.10421332)
61. Buchanan JB (1964) A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. *J Mar Biol Assoc UK* 44:565–576 [doi:10.1017/S0025315400027776](https://doi.org/10.1017/S0025315400027776)
62. Buchanan JB (1966) The biology of *Echinocardium cordatum* (Echinodermata: Spatangoidea) from different habitats. *J Mar Biol Assoc UK* 46:97–114 [doi:10.1017/S0025315400017574](https://doi.org/10.1017/S0025315400017574)
63. Buchanan JB (1967) Dispersion and demography of some infaunal echinoderm populations. *Symp Zool Soc Lond* 20:1–11
64. Budd GC 2004. *Brissopsis lyrifera* Spiny mudlark. In Tyler-Walters H., Hiscock K. (editors). *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. <https://dx.doi.org/10.17031/marlin.sp.1654.1>
65. Callaway R (2006) Tube worms promote community change. *Mar Ecol Prog Ser* 308:49–60 [doi:10.3354/meps308049](https://doi.org/10.3354/meps308049)
66. Cardoso JFMF, Witte JIJ, van der Veer HW (2007) Growth and reproduction of the bivalve *Spisula subtruncata* (da Costa) in Dutch coastal waters. *J Sea Res* 57:316–324 <https://doi.org/10.1016/j.seares.2006.12.002>
67. Cargnelli LM, Griesbach SJ, Packer DB, Weissberger E 1999. Essential fish habitat source document: Ocean Quahog, *Arctica islandica*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-148, 20 p.
68. Caron A, Boucher L, Desrosiers G, Retière C (1995) Population dynamics of the polychaete *Nephtys caeca* in an intertidal estuarine environment (Québec, Canada). 95). *J Mar Biol Assoc UK* 75:871–884 [doi:10.1017/S0025315400038212](https://doi.org/10.1017/S0025315400038212)
69. Caron A, Desrosiers G, Miron G, Retière C (1996) Comparison of spatial overlap between the polychaetes *Nereis virens* and *Nephtys caeca* in two intertidal estuarine environments. *Mar Biol* 124:537–550 [doi:10.1007/BF00351035](https://doi.org/10.1007/BF00351035)
70. Casaux C (1967) Développement larvaire de *Glycera convulata* Keferstein. *Vie Milieu* 18:559–572

71. Cazaux C (1968) Etude morphologique du développement larvaire d'annélides polychètes (Bassin d'Arca-chon). 1. Aphroditidae, Chrysopetalidae. *Arch Zool Exp Gén* 109:477–543
72. Cazaux C (1985) Reproduction et développement larvaire de l'annélide polychète saumâtre *Streblospio shrub-solii*. *Cah Biol Mar* 26:207–221
73. Chambers SJ, Woodham A (2003) A new species of *Chaetozone* (Polychaeta: Cirratulidae) from deep water in the northeast Atlantic, with comments on the diversity of the genus in cold northern waters. *Hydrobiologia* 496:41–48 [doi:10.1023/A:1026116008735](https://doi.org/10.1023/A:1026116008735)
74. Chanley P (1965) Larval development of the brackish water mastrid clam, *Rangia cuneata*. *Chesap Sci* 6:209–213 [doi:10.2307/1350815](https://doi.org/10.2307/1350815)
75. Chapman G (1965) The egg cocoons of *Scoloplos armiger* O. F. Müller. *Biol Bull* 128:189–197 [doi:10.2307/1539548](https://doi.org/10.2307/1539548)
76. Chartosia N, Kitsos MS, Koukouras A (2010) Seasonal diet of *Portunus latipes* (Pennant, 1777) (Decapoda, Portunidae). *Crustaceana* 83:1101–1113 [doi:10.1163/001121610X526951](https://doi.org/10.1163/001121610X526951)
77. Chatzinikolaou E, Richardson CA (2010) Parental size and environmental conditions affect egg capsule production by *Nassarius reticulatus* (Linnaeus 1758) (Gastropoda: Nassariidae). *J Exp Mar Biol Ecol* 390:14–21 [doi:10.1016/j.jembe.2010.04.029](https://doi.org/10.1016/j.jembe.2010.04.029)
78. Checa A, Harper EM, Willinger M (2012) Aragonitic dendritic prismatic shell microstructure in *Thracia* (Bivalvia, Anomalodesmata). *Invertebr Biol* 131:19–29 [doi:10.1111/j.1744-7410.2011.00254.x](https://doi.org/10.1111/j.1744-7410.2011.00254.x)
79. Chen PS (1958) Further studies on free amino-acids and peptides in eggs and embryos of different sea-urchin species and hybrids. *Experientia* 14:369–371 [PubMed doi:10.1007/BF02159160](https://pubmed.ncbi.nlm.nih.gov/159160/)
80. Chetoui I, Telahigue K, Bejaoui S, Rabeh I, Ghribi F, Denis F, El Cafsi M (2019) Annual reproductive cycle and condition index of *Macra corallina* (Mollusca: Bivalvia) from the north coast of Tunisia. *Invertebr Reprod Dev* 63:40–50 [doi:10.1080/07924259.2018.1529636](https://doi.org/10.1080/07924259.2018.1529636)
82. Choy SC (1986) Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Mar Ecol Prog Ser* 31:87–99 [doi:10.3354/meps031087](https://doi.org/10.3354/meps031087)
81. Choy S (1988) Reproductive Biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. *PSZNI: Mar Ecol* 9:227–241 [doi:10.1111/j.1439-0485.1988.tb00330.x](https://doi.org/10.1111/j.1439-0485.1988.tb00330.x)
83. Choy SC (1991) Embryonic and larval biology of *Liocarcinus holsatus* and *Necora puber* (Crustacea: brachy-ura: portunidae). *J Exp Mar Biol Ecol* 148:77–92 [doi:10.1016/0022-0981\(91\)90148-P](https://doi.org/10.1016/0022-0981(91)90148-P)
84. Christensen AM (1970) Feeding biology of *Astropecten*. *Ophelia* 8:1–134
85. Christie G (1982) The reproductive cycles of two species of *Pholoe* (Polychaeta: Sigalionidae) off the North-umberland coast. *Sarsia* 67:283–292 [doi:10.1080/00364827.1982.10421342](https://doi.org/10.1080/00364827.1982.10421342)
86. Christie G (1985) A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *J Mar Biol Assoc UK* 65:239–254 [doi:10.1017/S0025315400060938](https://doi.org/10.1017/S0025315400060938)
89. Clark RB (1962) Observations on the food of *Nephtys*. *Limnol Oceanogr* 7:380–385 [doi:10.4319/lo.1962.7.3.0380](https://doi.org/10.4319/lo.1962.7.3.0380)
87. Clark PF (1984) A comparative study of zoeal morphology in the genus *Liocarcinus* (Crustacea: Brachyura: Portunidae). *Zool J Linn Soc* 82:273–290 [doi:10.1111/j.1096-3642.1984.tb00644.x](https://doi.org/10.1111/j.1096-3642.1984.tb00644.x)
88. Clark R, Caudill CC (2001) Females of the marine amphipod *Jassa marmorata* mate multiple times with the same or different males. *Mar Freshwat Behav Physiol* 34:131–138 [doi:10.1080/10236240109379066](https://doi.org/10.1080/10236240109379066)
90. Conradi M, López-Gonzàles PJ, Bellan-Santini D (1995) A new species of *Urothoe* (Amphipoda, Gammar-idea) from the Iberian peninsula. *Cah Biol Mar* 36:9–13
91. Contreras-Guzmán RA, Puebla-Arce CE, Pacheco-Sánchez EG, Contreras-Saldaña FJ (2014) Growth and survival of *Gari solida* (Mollusca: Psammobiidae) D larvae, pediveliger larvae and postlarvae from conditioning broodstock. *Rev Biol Mar Oceanogr* 49:607–614 [doi:10.4067/S0718-19572014000300018](https://doi.org/10.4067/S0718-19572014000300018)

92. Cores Reyes C 2015. Biology, ecology and dynamics of Pennant's swimming crab (*Portumnus latipes*) in the South of Portugal. MSc thesis, University of Algarve, 111 p.
93. Corey S (1969) The comparative life histories of three Cumacea (Crustacea): *Cumopsis goodsiri* (Van Beneden), *Iphinoe trispinosa* (Goodsir), and *Pseudocuma longicornis* (Bate). *Can J Zool* 47:695–704 [doi:10.1139/z69-116](https://doi.org/10.1139/z69-116)
94. Corey S (1981) Comparative fecundity and reproductive strategies in seventeen species of the Cumacea (Crustacea: Peracarida). *Mar Biol* 62:65–72 [doi:10.1007/BF00396952](https://doi.org/10.1007/BF00396952)
95. Costa FO, Costa MH (1999) Life history of the amphipod *Gammarus locusta* in the Sado Estuary (Portugal). *Acta Oecol* 20:305–314 [doi:10.1016/S1146-609X\(99\)00136-8](https://doi.org/10.1016/S1146-609X(99)00136-8)
96. Cotter E, O'Riordan RM, Myers AA (2003) A histological study of reproduction in the serpulids *Pomatoceros triqueter* and *Pomatoceros lamarckii* (Annelida: Polychaeta). *Mar Biol* 142:905–914 [doi:10.1007/s00227-002-0987-2](https://doi.org/10.1007/s00227-002-0987-2)
97. Crawford GI (1937) Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *J Mar Biol Assoc UK* 21:631–643 [doi:10.1017/S0025315400053765](https://doi.org/10.1017/S0025315400053765)
98. Creaser EP Jr (1973) Reproduction of the bloodworm (*Glycera dibranchiata*) in the Sheepscot Estuary, Maine. *J Fish Res Board Can* 30:161–166 [doi:10.1139/f73-030](https://doi.org/10.1139/f73-030)
99. Creaser EP Jr, Clifford DA, Hogan MJ, Sampson DB 1983. A commercial sampling program for sandworms, *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine coast. NOAA Technical Report NMFS SSRF-767, National Oceanic and Atmospheric Administration, USA, 55 p.
100. Criales MM, Anger K (1986) Experimental studies on the larval development of the shrimps *Crangon crangon* and *C. Allmanni*. *Helgol Meeresunters* 40:241–265 [doi:10.1007/BF01983735](https://doi.org/10.1007/BF01983735)
101. Crothers JH (1967) The biology of the shore crab *Carcinus maenas* (L.) 1. The background-anatomy, growth and life history. *Field Stud* 2:407–434
102. Curtis MA (1977) Life cycles and population dynamics of marine benthic polychaetes from the Disko Bay area of West Greenland. *Ophelia* 16:9–58 [doi:10.1080/00785326.1977.10425460](https://doi.org/10.1080/00785326.1977.10425460)
103. D'Andrea AF, Lopez GR, Aller RC (2004) Rapid physical and biological particle mixing on an intertidal sandflat. *J Mar Res* 62:67–92 [doi:10.1357/00222400460744627](https://doi.org/10.1357/00222400460744627)
104. da Costa F, Darriba S, Martínez-Patiño D (2008) Embryonic and larval development of *Ensis arcuatus* (Jeffreys, 1865) (Bivalvia: Pharidae). *J Molluscan Stud* 74:103–109 [doi:10.1093/mollus/eym051](https://doi.org/10.1093/mollus/eym051)
105. da Costa FD, Martínez-Patiño D, Ojea J, Nóvoa S (2010) Larval rearing and spat production of the razor clam *Ensis siliqua* (Bivalvia: Pharidae). *J Shellfish Res* 29:347–351 [doi:10.2983/035.029.0209](https://doi.org/10.2983/035.029.0209)
106. Dahm C (1993) Growth, production and ecological significance of *Ophiura albida* and *O. ophiura* (Echinodermata: Ophiuroidea) in the German Bight. *Mar Biol* 116:431–437 [doi:10.1007/BF00350060](https://doi.org/10.1007/BF00350060)
108. Dales RP (1950) The reproduction and larval development of *Nereis diversicolor* O. F. Müller. *J Mar Biol Assoc UK* 29:321–359 [doi:10.1017/S0025315400055405](https://doi.org/10.1017/S0025315400055405)
109. Dales RP (1951) Notes on the reproduction and early development of the cirratulid *Tharyx marioni* (St Joseph). *J Mar Biol Assoc UK* 30:113–117 [doi:10.1017/S0025315400012613](https://doi.org/10.1017/S0025315400012613)
107. Dales RP (1957) The feeding mechanism and structure of the gut of *Owenia fusiformis* delle Chiaje. *J Mar Biol Assoc UK* 36:81–89 [doi:10.1017/S0025315400017082](https://doi.org/10.1017/S0025315400017082)
110. Daly JM (1972) The maturation and breeding biology of *Harmothoe imbricata* (Polychaeta: Polynoidae). *Mar Biol* 12:53–66
111. Dando PR, Southward AJ, Southward EC (1986) Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proc R Soc Lond B Biol Sci* 227:227–247 [doi:10.1098/rspb.1986.0021](https://doi.org/10.1098/rspb.1986.0021)
112. Daro MH, Polk P (1973) The autecology of *Polydora ciliata* along the Belgian coast. *Neth J Sea Res* 6:130–140 [doi:10.1016/0077-7579\(73\)90008-2](https://doi.org/10.1016/0077-7579(73)90008-2)

113. Dauer DM (1983) Functional morphology and feeding behavior of *Scolecopsis squamata* (Polychaeta: Spionidae). *Mar Biol* 77:279–285 [doi:10.1007/BF00395817](https://doi.org/10.1007/BF00395817)
114. Dauer DM, Maybury CA, Ewing M (1981) Feeding behaviour and functional ecology of several spionid polychaetes from the Chesapeake bay. *J Exp Mar Biol Ecol* 54:21–38 [doi:10.1016/0022-0981\(81\)90100-3](https://doi.org/10.1016/0022-0981(81)90100-3)
115. Dauvin JC (1988) Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 1. *Ampelisca tenuicornis* Liljeborg. *J Exp Mar Biol Ecol* 118:55–84 [doi:10.1016/0022-0981\(88\)90122-0](https://doi.org/10.1016/0022-0981(88)90122-0)
116. Dauvin JC (1988) Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 2. *Ampelisca brevicornis* (Costa). *J Exp Mar Biol Ecol* 119:213–233 [doi:10.1016/0022-0981\(88\)90194-3](https://doi.org/10.1016/0022-0981(88)90194-3)
117. Dauvin JC, Gentil F (1989) Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (Western English Channel). *Mar Biol* 103:63–73 [doi:10.1007/BF00391065](https://doi.org/10.1007/BF00391065)
118. Dauwe B, Herman PMJ, Heip CHR (1998) Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Mar Ecol Prog Ser* 173:67–83 [doi:10.3354/meps173067](https://doi.org/10.3354/meps173067)
119. Davis JP, Wilson JG (1983) The population structure and ecology of *Nucula turgida* (Leckenby & Marshall) in Dublin Bay. *Progress in Underwater Science* 8:53–60
120. Dawirs RR (1979) Effects of temperature and salinity on larval development of *Pagurus bernhardus* (Decapoda, Paguridae). *Mar Ecol Prog Ser* 1:323–329 [doi:10.3354/meps001323](https://doi.org/10.3354/meps001323)
121. Day JH (1934) Development of *Scolecopsis fuliginosa* (Claparède). *J Mar Biol Assoc UK* 19:633–654 [doi:10.1017/S0025315400046671](https://doi.org/10.1017/S0025315400046671)
122. Day JH, Wilson DP (1934) On the relation of the substratum to the metamorphosis of *Scolecopsis fuliginosa* (Claparède). *J Mar Biol Assoc UK* 19:655–662 [doi:10.1017/S0025315400046683](https://doi.org/10.1017/S0025315400046683)
123. Nunes C, Nunes P, Jangoux M (2004) Reproductive cycle of the spatangoid echinoid *Echinocardium cordatum* (Echinodermata) in the southwestern North Sea. *Invertebr Reprod Dev* 45:41–57 [doi:10.1080/07924259.2004.9652572](https://doi.org/10.1080/07924259.2004.9652572)
124. Nunes C, Jangoux M (2007) Larval growth and perimetamorphosis in the echinoid *Echinocardium cordatum* (Echinodermata): the spatangoid way to become a sea urchin. *Zoomorphology* 126:103–119 [doi:10.1007/s00435-007-0032-6](https://doi.org/10.1007/s00435-007-0032-6)
125. de Bruyne R, van Leeuwen S, Gmelig Meyling A, Daan R 2013. Schelpdieren van het Nederlandse Noordzeegebied. Tirion Uitgevers, Utrecht, Nederland, 414 p.
126. de Schweinitz EH, Lutz RA (1976) Larval development of the northern horse mussel, *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. *Biol Bull* 150:348–360 [PubMed doi:10.2307/1540677](https://pubmed.ncbi.nlm.nih.gov/1540677/)
127. de Vooy CGN (1999) Numbers of larvae and primary plantigrades of the mussel *Mytilus edulis* in the western Dutch Wadden Sea. *J Sea Res* 41:189–201 [doi:10.1016/S1385-1101\(98\)00049-5](https://doi.org/10.1016/S1385-1101(98)00049-5)
128. Deart YV, Frolov AA, Manushin IE (2013) Bivalves *Abra prismatica* (Montagu, 1808) and *Gari fervensis* (Gmelin, 1791)—Species new to the fauna of the Russian sector of the Barents Sea. *Russ J Biol Invasions* 4:139–148 [doi:10.1134/S2075111713030028](https://doi.org/10.1134/S2075111713030028)
130. Dekker R, Beukema JJ (1993) Dynamics and growth of a bivalve, *Abra tenuis*, at the northern edge of its distribution. *J Mar Biol Assoc UK* 73:497–511 [doi:10.1017/S0025315400033063](https://doi.org/10.1017/S0025315400033063)
129. Dekker R, Beukema J (1999) Relations of summer and winter temperatures with dynamics and growth of two bivalves, *Tellina tenuis* and *Abra tenuis*, on the northern edge of their intertidal distribution. *J Sea Res* 42:207–220 [doi:10.1016/S1385-1101\(99\)00026-X](https://doi.org/10.1016/S1385-1101(99)00026-X)
131. Delaunois N, Sheridan R (1989) Studies on the biology of Turridae on European coasts: *Mangelia nebula* (Montagu). *Cah Biol Mar* 30:347–359

132. Delgado L, Guerao G, Ribera C (1997) Biology of the mysid *Mesopodopsis slabberi* (van Beneden, 1861) (Crustacea, Mysidacea) in a coastal lagoon of the Ebro delta (NW Mediterranean). *Hydrobiologia* 357:27–35 [doi:10.1023/A:1003118332417](https://doi.org/10.1023/A:1003118332417)
133. Delgado M, Silva L, Juárez A (2013) Aspects of reproduction of striped venus *Chamelea gallina* in the Gulf of Cádiz (SW Spain): implications for fishery management. *Fish Res* 146:86–95 [doi:10.1016/j.fishres.2013.04.005](https://doi.org/10.1016/j.fishres.2013.04.005)
134. Dennell R (1933) The habits and feeding mechanism of the Amphipod *Haustorius arenarius* Slabber. *Journal of the Linnean Society of London. Zoology* 38:363–388
135. Dennell R (1934) The feeding mechanism of the cumacean crustacean *Diastylis bradyi*. *Trans R Soc Edinb* 58:125–142 [doi:10.1017/S0080456800023073](https://doi.org/10.1017/S0080456800023073)
136. Desdevises Y, Maillet V, Fuentes M, Escriba H (2011) A snapshot of the population structure of *Branchiostoma lanceolatum* in the Racou Beach, France, during its spawning season. *PLoS One* 6:e18520 [PubMed](https://pubmed.ncbi.nlm.nih.gov/218520/) [doi:10.1371/journal.pone.0018520](https://doi.org/10.1371/journal.pone.0018520)
137. Desroy N, Retière C, Thiébaud E (1998) Infaunal predation regulates benthic recruitment: an experimental study of the influence of the predator *Nephtys hombergii* (Savigny) on recruits of *Nereis diversicolor* (O.F. Müller). *J Exp Mar Biol Ecol* 228:257–272 [doi:10.1016/S0022-0981\(98\)00033-1](https://doi.org/10.1016/S0022-0981(98)00033-1)
138. Donn TE Jr, Croker RA (1983) Production ecology of *Haustorius canadensis* (Amphipoda: Haustoriidae) in southern Maine. *Developments in Hydrobiology* 19:661–667
139. Dorgan KM, D’Amelio C, Lindsay SM (2016) Strategies of burrowing in soft muddy sediments by diverse polychaetes. *Invertebr Biol* 135:287–301 [doi:10.1111/ivb.12131](https://doi.org/10.1111/ivb.12131)
140. Dorresteijn AWC, Westheide W (eds) 1999. *Reproductive Strategies and Developmental Patterns in Annelids*. Springer, Vol 142 of *Developments in Hydrobiology*, 1st edition.
141. Duchêne J.C., 1977. Données sur le cycle biologique de la polychète sédentaire *Terebellides stroemii* (Terebellidae) dans la région de Banyuls-sur-Mer. *Comptes rendus de l'académie des sciences de Paris, série D* 284:2543–2546. unknown
142. Duineveld GCA, Künitzer A, Heyman RP (1987) *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the North Sea. Distribution, present and former abundance and size composition. *Neth J Sea Res* 21:317–329 [doi:10.1016/0077-7579\(87\)90006-8](https://doi.org/10.1016/0077-7579(87)90006-8)
143. Dupont S, Mallefet J (2000) Luminous capabilities and life-history traits of the polychromatic ophiuroid *Amphipholis squamata* in two isolated populations from Oliveri-Tindari lagoon system, Sicily. *Hydrobiologia* 440:137–144 [doi:10.1023/A:1004154707305](https://doi.org/10.1023/A:1004154707305)
144. Dutertre M, Hamon D, Chevalier C, Ehrhold A (2013) The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES J Mar Sci* 70:294–308 [doi:10.1093/icesjms/fss170](https://doi.org/10.1093/icesjms/fss170)
145. Duval M (1963) The biology of *Petricola pholadiformis* Lamark (Lamellibranchiata Petricolidae). *J Molluscan Stud* 35:89–100 [doi:10.1093/oxfordjournals.mollus.a064906](https://doi.org/10.1093/oxfordjournals.mollus.a064906)
146. Dworschak PC (1998) Observations on the biology of the burrowing mud shrimps *Callinassa tyrrhena* and *C. candida* (Decapoda: Thalassinidea). *J Nat Hist* 32:1535–1548 [doi:10.1080/00222939800771071](https://doi.org/10.1080/00222939800771071)
147. Eckberg WR, Hill SD 1996. *Chaetopterus* - Oocyte maturation, early development, and regeneration. *Marine Models Electronic Record* <http://www.mbl.edu/BiologicalBulletin/mmer.html>
148. Elwood RW, Stewart A (1987) Reproduction in the littoral hermit crab *Pagurus bernhardus*. *Ir Nat J* 22:252–255
149. Emig CC (1982) The biology of Phoronida. *Adv Mar Biol* 19:1–89 [doi:10.1016/S0065-2881\(08\)60086-3](https://doi.org/10.1016/S0065-2881(08)60086-3)
150. Emson RH (1977) The feeding and consequent role of *Eulalia viridis* (O. F. Müller) (Polychaeta) in intertidal communities. *J Mar Biol Assoc UK* 57:93–96 [doi:10.1017/S0025315400021251](https://doi.org/10.1017/S0025315400021251)

151. Emson RH, Whitfield PJ (1989) Aspects of the life history of a tide pool population of *Amphipholis squamata* (Ophiuroidea) from South Devon. *J Mar Biol Assoc UK* 69:27–41 [doi:10.1017/S0025315400049080](https://doi.org/10.1017/S0025315400049080)
152. Enders HE (1909) A study of the life-history and habits of *Chaetopterus variopedatus* Renier et Claparede. *J Morphol* 20:479–531 [doi:10.1002/jmor.1050200306](https://doi.org/10.1002/jmor.1050200306)
153. Erdoğan-Dereli D, Çınar ME (2020) *Paraonis fulgens* (Annelida: Paraonidae), a new species record for the marine fauna of Turkey. *Ege Journal of Fisheries and Aquatic Sciences* 37:181–185 [doi:10.12714/egejfas.37.2.09](https://doi.org/10.12714/egejfas.37.2.09)
154. Esselink P, Zwarts L (1989) Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Mar Ecol Prog Ser* 56:243–254 [doi:10.3354/meps056243](https://doi.org/10.3354/meps056243)
155. Faasse M, Stikvoort E (2002) Mariene en estuariene vlokreeftjes van zachte bodems in het Deltagebied (Crustacea: Gammaridea). *Nederlandse Faunistische Mededelingen* 17:57–86
156. Faasse M, van Moorsel G (2000) Nieuwe en minder bekende vlokreeftjes van sublitorale harde bodems in het Deltagebied (Crustacea: Amphipoda: Gammaridea). *Nederlandse Faunistische Mededelingen* 11:19–44
158. Fahy E, Gaffney J (2001) Growth statistics of an exploited razor clam (*Ensis siliqua*) bed at Gormanstown, Co Meath, Ireland. *Hydrobiologia* 465:139–151 [doi:10.1023/A:1014580522523](https://doi.org/10.1023/A:1014580522523)
157. Fahy E, Carrol J, O’Toole M (2003) A preliminary account of fisheries for the surf clam *Spisula solida* (L) (Mactracea) in Ireland. *Irish Fisheries Bulletin* 21:1–27
159. Falk-Petersen IB (1982) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway. *Sarsia* 67:69–78 [doi:10.1080/00364827.1982.10421335](https://doi.org/10.1080/00364827.1982.10421335)
160. Farke H (1979) Population dynamics, reproduction and early development of *Tharyx marioni* (Polychaeta, Cirratulidae) on tidal flats of the German Bight. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 18:69–99
161. Farmer ASD (1974) Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). *J Zool* 174:161–183 [doi:10.1111/j.1469-7998.1974.tb03150.x](https://doi.org/10.1111/j.1469-7998.1974.tb03150.x)
162. Farmer ASD (1975) Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). *FAO Fish Synop* 112:1–97
163. Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
164. Fenaux L (1970) Maturation of the gonads and seasonal cycle of the planktonic larvae of the ophiuroid *Amphiura chiajei* Forbes. *Biol Bull* 138:262–271 [doi:10.2307/1540211](https://doi.org/10.2307/1540211)
165. Fernández L, González-Gurriarán E, Freire J (1991) Population biology of *Liocarcinus depurator* (Brachyura: Portunidae) in mussel raft culture areas in the Ría De Arousa (Galicia, Nw Spain). *J Mar Biol Assoc UK* 71:375–390 [doi:10.1017/S0025315400051651](https://doi.org/10.1017/S0025315400051651)
166. Ferrand JG, Vadon C, Doumenc D, Guille A (1988) The effect of depth on the reproductive cycle of *Brissopsis lyrifera* (Echinoidea, Echinodermata) in the Gulf of Lions, Mediterranean Sea. *Mar Biol* 99:387–392 [doi:10.1007/BF02112131](https://doi.org/10.1007/BF02112131)
167. Fiege D, Kröncke I, Barnich R (2000) High abundance of *Myriochele fragilis* Nilsen & Holthe, 1985 (Polychaeta: Oweniidae) in the deep sea of the Eastern Mediterranean. *Hydrobiologia* 426:97–103 [doi:10.1023/A:1003947318925](https://doi.org/10.1023/A:1003947318925)
168. Fincham AA (1971) Ecology and population studies of some intertidal and sublittoral sand-dwelling amphipods. *J Mar Biol Assoc UK* 51:471–488 [doi:10.1017/S0025315400031921](https://doi.org/10.1017/S0025315400031921)
173. Fish S (1970) The biology of *Eurydice pulchra* (Crustacea: Isopoda). *J Mar Biol Assoc UK* 50:753–768 [doi:10.1017/S0025315400005026](https://doi.org/10.1017/S0025315400005026)
169. Fish JD (1975) Development, hatching and brood size in *Bathyporeia pilosa* and *B. pelagica* (Crustacea: Amphipoda). *J Mar Biol Assoc UK* 55:357–368 [doi:10.1017/S002531540001599X](https://doi.org/10.1017/S002531540001599X)

170. Fish JD, Fish S (1977) The veliger larva of *Hydrobia ulvae* with observations on the veliger of *Littorina littorea* (Mollusca: Prosobranchia). *J Zool* 182:495–503 [doi:10.1111/j.1469-7998.1977.tb04165.x](https://doi.org/10.1111/j.1469-7998.1977.tb04165.x)
171. Fish JD, Fish S 2011. A student's guide to the seashore. Third edition. Cambridge University Press, 527 p.
172. Fish JD, Mills A (1979) The reproductive biology of *Corophium volutator* and *C. arenarium* (Crustacea: Amphipoda). *J Mar Biol Assoc UK* 59:355–368 [doi:10.1017/S002531540004265X](https://doi.org/10.1017/S002531540004265X)
174. Franke HD (1999) Reproduction of the Syllidae (Annelida: Polychaeta). *Hydrobiologia* 402:39–55 [doi:10.1023/A:1003732307286](https://doi.org/10.1023/A:1003732307286)
175. Franke HD, Beermann J (2014) The influence of intrinsic and extrinsic factors on developmental parameters and their relationships in the marine isopod *Idotea linearis* (Crustacea). *Hydrobiologia* 732:197–212 [doi:10.1007/s10750-014-1846-0](https://doi.org/10.1007/s10750-014-1846-0)
176. Franzén Å (1982) Ultrastructure of spermatids and spermatozoa in three polychaetes with modified biology of reproduction: *Autolytus* sp., *Chitinopoma serrula*, and *Capitella capitata*. *International Journal of Invertebrate Reproduction* 5:185–200 [doi:10.1080/01651269.1982.10553469](https://doi.org/10.1080/01651269.1982.10553469)
177. Freeman SM, Richardson CA, Seed R (2001) Seasonal abundance, spatial distribution, spawning and growth of *Astropecten irregularis* (Echinodermata: Asteroidea). *Estuar Coast Shelf Sci* 53:39–49 [doi:10.1006/ecss.2000.0758](https://doi.org/10.1006/ecss.2000.0758)
178. Freire J (1996) Feeding ecology of *Liocarcinus depurator* (Decapoda: Portunidae) in the Ria de Arousa (Galicia, north-west Spain): effects of habitat, season and life history. *Mar Biol* 126:297–311 [doi:10.1007/BF00347454](https://doi.org/10.1007/BF00347454)
179. Fretter V, Graham A (1954) Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *J Mar Biol Assoc UK* 33:565–585 [doi:10.1017/S0025315400026862](https://doi.org/10.1017/S0025315400026862)
180. Fuentes M, Benito E, Bertrand S, Paris M and others (2007) Insights into spawning behavior and development of the European Amphioxus (*Branchiostoma lanceolatum*). *J Exp Zool* 308B:484–493 [PubMed doi:10.1002/jez.b.21179](https://pubmed.ncbi.nlm.nih.gov/10.1002/jez.b.21179/)
181. Gage J (1966) The life-histories of the bivalves *Montacuta substriata* and *M. ferruginosa*, 'commensals' with spatangoids. *J Mar Biol Assoc UK* 46:499–511 [doi:10.1017/S0025315400033300](https://doi.org/10.1017/S0025315400033300)
182. Garcia C 2010. Approche fonctionnelle des communautés benthiques du bassin oriental de la Manche et du sud de la mer du Nord. PhD thesis, Université de Lille, 399 p.
183. Garraffoni ARS, Yokoyama LQ, Amaral ACZ (2014) The gametogenic cycle and life history of *Nicolea uspiana* (Polychaeta: Terebellidae) on the south-east coast of Brazil. *J Mar Biol Assoc UK* 94:925–933 [doi:10.1017/S0025315414000149](https://doi.org/10.1017/S0025315414000149)
184. Garwood PR (1982) The life-cycle and population dynamics of *Streptosyllis websteri* (polychaeta: syllidae) from a Northumberland beach. *J Mar Biol Assoc UK* 62:783–798 [doi:10.1017/S0025315400044052](https://doi.org/10.1017/S0025315400044052)
185. Gaston GR, McLelland JA, Heard RW (1992) Feeding biology, distribution, and ecology of two species of benthic polychaetes: *Paraonis fulgens* and *Paraonis pygoenigmatica* (Polychaeta: Paraonidae). *Gulf Res Rep* 8:395–399
187. Gentil F, Zakardjian B 1990. Reproductive cycle of the ophiuroid *Acrocroca brachiata* (Montagu) in the Bay of Seine (English Channel). In: Echinoderm research, Proceedings of the 2nd European Conference on Echinoderms. De Ridder C., Dubois P., Lahaye M.C., Jangoux M. (editors), Brussels, Belgium, 19-21 September 1989. Balkema, Rotterdam, pp 83–89.
186. Gentil F, Dauvin JC, Ménard F (1990) Reproductive biology of the polychaete *Owenia fusiformis* Delle Chiaje in the Bay of Seine (eastern English Channel). *J Exp Mar Biol Ecol* 142:13–23 [doi:10.1016/0022-0981\(90\)90134-X](https://doi.org/10.1016/0022-0981(90)90134-X)
188. Ghiold J (1982) Observations on the clypeasteriid *Echinocyamus pusillus* (O.F. Müller). *J Exp Mar Biol Ecol* 61:57–74 [doi:10.1016/0022-0981\(82\)90021-1](https://doi.org/10.1016/0022-0981(82)90021-1)
189. Giangrande A (1997) Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanogr Mar Biol Annu Rev* 35:323–386

190. Giangrande A, Fraschetti S (1993) Life cycle, growth and secondary production in a brackish-water population of the polychaete *Notomastus latericeus* (Capitellidae) in the Mediterranean Sea. *PSZNI: Mar Ecol* 14:313–327 [doi:10.1111/j.1439-0485.1993.tb00003.x](https://doi.org/10.1111/j.1439-0485.1993.tb00003.x)
191. Gibbs PE (1968) Observations on the population of *Scoloplos armiger* at Whitstable. *J Mar Biol Assoc UK* 48:225–254 [doi:10.1017/S0025315400032550](https://doi.org/10.1017/S0025315400032550)
192. Gibbs PE (1971) A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *J Mar Biol Assoc UK* 51:745–769 [doi:10.1017/S002531540001794X](https://doi.org/10.1017/S002531540001794X)
193. Gibbs PE (1984) The Population cycle of the bivalve *Abra tenuis* and its mode of reproduction. *J Mar Biol Assoc UK* 64:791–800 [doi:10.1017/S0025315400047238](https://doi.org/10.1017/S0025315400047238)
194. Gibbs PE, Langston WJ, Burt GR, Pascoe PL (1983) *Tharyx marioni* (Polychaeta): a remarkable accumulator of arsenic. *J Mar Biol Assoc UK* 63:313–325 [doi:10.1017/S0025315400070703](https://doi.org/10.1017/S0025315400070703)
195. Giese AC, Pearse JS (eds) 1977. Reproduction of marine invertebrates. Volume III. Annelids and Echiurans. New York-San Francisco-London: Academic Press. 343 p.
196. Giese AC, Pearse JS (eds) 1977. Reproduction of marine invertebrates. Volume IV. Molluscs: Gastropods and Cephalopods. New York-San Francisco-London: Academic Press, 369 p.
197. Giglioli MEC (1955) The egg masses of the Naticidae (Gastropoda). *J Fish Res Bd Can* 12:287–327 [doi:10.1139/f55-018](https://doi.org/10.1139/f55-018)
198. Gillet P, Gorman E (2002) Population structure and secondary production of *Heteromastus fliformis* (Polychaeta: Capitellidae) in the Loire estuary, France. *J Mar Biol Assoc UK* 82:395–402 [doi:10.1017/S0025315402005635](https://doi.org/10.1017/S0025315402005635)
199. Lo Giudice Cappelli E, Austin WEN (2020) Marine bivalve feeding strategies and radiocarbon ages in north-east Atlantic coastal waters. *Radiocarbon* 62:107–125 [doi:10.1017/RDC.2019.68](https://doi.org/10.1017/RDC.2019.68)
200. Grant A, Tyler PA (1986) An analysis of the reproductive pattern in the sea star *Astropecten irregularis* (Pennant) from the Bristol Channel. *Journal International Journal of Invertebrate Reproduction and Development* 9:345–361 [doi:10.1080/01688170.1986.10510211](https://doi.org/10.1080/01688170.1986.10510211)
201. Grémare A (1986) A comparative study of reproductive energetics in two populations of the terebellid polychaete *Eupolyornia nebulosa* Montagu with different reproductive modes. *J Exp Mar Biol Ecol* 96:287–302 [doi:10.1016/0022-0981\(86\)90208-X](https://doi.org/10.1016/0022-0981(86)90208-X)
203. Grémare A, Olive PJW (1986) A preliminary study of fecundity and reproductive effort in two polychaetous annelids with contrasting reproductive strategies. *International Journal of Invertebrate Reproduction and Development* 9:1–16 [doi:10.1080/01688170.1986.10510176](https://doi.org/10.1080/01688170.1986.10510176)
202. Grémare A, Amouroux JM, Amouroux J (1989) Modelling of consumption and assimilation in the deposit-feeding polychaete *Eupolyornia nebulosa*. *Mar Ecol Prog Ser* 54:239–248 [doi:10.3354/meps054239](https://doi.org/10.3354/meps054239)
204. Griffi CL, Richardson CA (2006) Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *J Exp Mar Biol Ecol* 331:91–98 [doi:10.1016/j.jembe.2005.10.002](https://doi.org/10.1016/j.jembe.2005.10.002)
205. Grobe P 2008. Larval development, the origin of the coelom and the phylogenetic relationships of the Phoronida. PhD thesis, Freie Universiteit Berlin, 90 p.
206. Gros O, Duplessis MR, Felbeck H (1999) Embryonic development and endosymbiont transmission mode in the symbiotic clam *Lucinoma aequizonata* (Bivalvia: lucinidae). *Invertebr Reprod Dev* 36:93–103 [doi:10.1080/07924259.1999.9652683](https://doi.org/10.1080/07924259.1999.9652683)
207. Gudmundsson H (1985) Life history patterns of polychaete species of the family Spionidae. *J Mar Biol Assoc UK* 65:93–111 [doi:10.1017/S0025315400060835](https://doi.org/10.1017/S0025315400060835)
208. Guérin JP (1972) Rapports taxonomiques et développement larvaire de *Spio decoratus* Bobretzky 1871 (Annelide Polychète). *Cah Biol Mar* 13:321–339

209. Guerra-García JM, Tierno de Figueroa JM, Navarro-Barranco C, Ros M, Sánchez-Moyano JE, Moreira J (2014) Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. *J Sea Res* 85:508–517 [doi:10.1016/j.seares.2013.08.006](https://doi.org/10.1016/j.seares.2013.08.006)
210. Guillou J, Sauriau PG (1985) Some observations on the biology and ecology of a *Venus striatula* population in the bay of Douardenez, Brittany. *J Mar Biol Assoc UK* 65:889–900 [doi:10.1017/S0025315400019391](https://doi.org/10.1017/S0025315400019391)
211. Haaland B, Schram TA (1983) Larval development and metamorphosis of *Ophiodromus flexuosus* (Delle Chiaje) (Hesionidae, Polychaeta). *Sarsia* 68:85–96 [doi:10.1080/00364827.1983.10420560](https://doi.org/10.1080/00364827.1983.10420560)
212. Hagström BE (1956) Studies on the fertilization of jelly-free sea urchin eggs. *Exp Cell Res* 10:24–28 [PubMed doi:10.1016/0014-4827\(56\)90066-0](https://pubmed.ncbi.nlm.nih.gov/1016/0014-4827(56)90066-0/)
213. Hanks RW 1969. The genus *Sphenia* (Pelecypoda, Mollusca) in the western North Atlantic, with observations on other Myidae. PhD thesis, University of New Hampshire, 94 p.
214. Hannan CA 1980. The life histories and population dynamics of the polychaetes, *Nothria elegans* (Johnson) (Onuphidae) and *Magelona sacculata* Hartman (magelonidae) in Monterey bay, California. Master thesis, San Jose State University, 118 p.
215. Hansen B (1993) Aspects of feeding, growth and stage development by trochophora larvae of the boreal polychaete *Mediomastus fragile* (Rasmussen) (Capitellidae). *J Exp Mar Biol Ecol* 166:273–288 [doi:10.1016/0022-0981\(93\)90224-C](https://doi.org/10.1016/0022-0981(93)90224-C)
216. Hartnoll RG (1968) Reproduction in the burrowing crab, *Corystes cassivelaunus* (Pennant, 1777) (Decapoda, Brancyura). *Crustaceana* 15:165–170 [doi:10.1163/156854068X01024](https://doi.org/10.1163/156854068X01024)
217. Hartnoll RG, Mohamedeen H (1987) Laboratory growth of the larvae of six British crabs. *J Exp Mar Biol Ecol* 107:155–170 [doi:10.1016/0022-0981\(87\)90193-6](https://doi.org/10.1016/0022-0981(87)90193-6)
218. Hayward PJ, Ryland JS (eds) 2017. Handbook of the Marine Fauna of North-West Europe. Second Edition. Oxford University Press, 785 p.
219. Heffernan P (1985) Demography of *Pholoe minuta* (Polychaeta: Sigalionidae) in Galway Bay, west coast of Ireland, with special reference to settlement and recruitment patterns. *Mar Biol* 84:323–329 [doi:10.1007/BF00392502](https://doi.org/10.1007/BF00392502)
220. Heffernan P, Keegan BF (1988) The larval development of *Pholoe minuta* (Polychaeta: Sigalionidae) in Galway Bay, Ireland. *J Mar Biol Assoc UK* 68:339–350 [doi:10.1017/S0025315400052231](https://doi.org/10.1017/S0025315400052231)
221. Heffernan P, O'Connor B, Keegan BF (1983) Population dynamics and reproductive cycle of *Pholoe minuta* (Polychaeta: Sigalionidae) in Galway Bay. *Mar Biol* 73:285–291 [doi:10.1007/BF00392254](https://doi.org/10.1007/BF00392254)
222. Henderson PA, Holmes RHA (1987) On the population biology of the common shrimp *Crangon crangon* (L.) (Crustacea: Caridea) in the Severn Estuary and Bristol Channel. *J Mar Biol Assoc UK* 67:825–847 [doi:10.1017/S0025315400057076](https://doi.org/10.1017/S0025315400057076)
223. Henderson SM, Richardson CA (1994) A comparison of the age, growth rate and burrowing behaviour of the razor clams, *Ensis siliqua* and *E. ensis*. *J Mar Biol Assoc UK* 74:939–954 [doi:10.1017/S0025315400090160](https://doi.org/10.1017/S0025315400090160)
224. Hernández-Otero A, Martínez-Castro C, Vázquez E, Macho G (2014) Reproductive cycle of *Ensis magnus* in the Ría de Pontevedra (NW Spain): spatial variability and fisheries management implications. *J Sea Res* 91:45–57 [doi:10.1016/j.seares.2014.04.008](https://doi.org/10.1016/j.seares.2014.04.008)
225. Herry A, Le Pennec M (1987) Endosymbiotic bacteria in the gills of the littoral bivalve molluscs *Thyasira flexuosa* (Thyasiridae) and *Lucinella divaricata* (Lucinidae). *Symbiosis* 4:25–36
226. Hill AE (1990) Pelagic dispersal of Norway lobster *Nephrops*. *Mar Ecol Prog Ser* 64:217–226 [doi:10.3354/meps064217](https://doi.org/10.3354/meps064217)
227. Hily C (1987) Spatio-temporal variability of *Chaetozone setosa* (Malmgren) populations on an organic gradient in the Bay of Brest, France. *J Exp Mar Biol Ecol* 112:201–216 [doi:10.1016/0022-0981\(87\)90069-4](https://doi.org/10.1016/0022-0981(87)90069-4)
228. Holland ND, Holland LZ (1991) The fine structure of the growth stage oocytes of a lancelet (= *Amphioxus*), *Branchiostoma lanceolatum*. *Invertebr Reprod Dev* 19:107–122 [doi:10.1080/07924259.1991.9672164](https://doi.org/10.1080/07924259.1991.9672164)

229. Hollertz K, Duchêne JC (2001) Burrowing behaviour and sediment reworking in the heart urchin *Brissopsis lyrifera* Forbes (Spatangoida). *Mar Biol* 139:951–957 [doi:10.1007/s002270100629](https://doi.org/10.1007/s002270100629)
230. Hollertz K, Sköld M, Rosenberg R (1998) Interactions between two deposit feeding echinoderms: the spatangoid *Brissopsis lyrifera* (Forbes) and the ophiuroid *Amphiura chiajei* Forbes. *Hydrobiologia* 375–376:287–295 [doi:10.1023/A:1017013123372](https://doi.org/10.1023/A:1017013123372)
231. Holtmann SE, Groenewold A, Schrader KHM, Asjes J and others 1996. Atlas of the zoobenthos of the Dutch continental shelf. Ministry of Transport, Public Works and Water Management: Rijswijk, The Netherlands, 243 p.
232. Honkoop PJC, van der Meer J (1998) Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. *J Exp Mar Biol Ecol* 220:227–246 [doi:10.1016/S0022-0981\(97\)00107-X](https://doi.org/10.1016/S0022-0981(97)00107-X)
233. Hrs-Brenko M (2006) The basket shell, *Corbula gibba* Olivi, 1792 (Bivalve Mollusks) as a species resistant to environmental disturbances: a review. *Acta Adriat* 47:49–64
234. Hughes TG (1973) Deposit feeding in *Abra tenuis* (Bivalvia: Tellinacea). *J Zool* 171:499–512 [doi:10.1111/j.1469-7998.1973.tb02232.x](https://doi.org/10.1111/j.1469-7998.1973.tb02232.x)
235. Humphreys WJ (1962) Electron microscope studies on eggs of *Mytilus edulis*. *J Ultrastruct Res* 7:467–487 [PubMed doi:10.1016/S0022-5320\(62\)90041-2](https://pubmed.ncbi.nlm.nih.gov/doi/10.1016/S0022-5320(62)90041-2)
236. Ingle RW, Rice AL (1971) The larval development of the masked crab, *Corystes cassivelaunus* (Pennant) (Brachyura, Corystidae), reared in the laboratory. *Crustaceana* 20:271–284 [doi:10.1163/156854069X00213](https://doi.org/10.1163/156854069X00213)
237. Irlinger JP, Gentil F, Quintino V (1991) Reproductive biology of the polychaete *Pectinaria koreni* (Malgrem) in the Bay of Seine (English channel). *Ophelia* 5:343–350
238. Jensen KT, Kristensen LD (1990) A field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. *J Exp Mar Biol Ecol* 137:1–24 [doi:10.1016/0022-0981\(90\)90057-J](https://doi.org/10.1016/0022-0981(90)90057-J)
239. Jeong SJ, Yu OH, Suh HL (2009) Reproductive patterns and secondary production of *Gammaropsis japonicus* (Crustacea, Amphipoda) on the seagrass *Zostera marina* of Korea. *Hydrobiologia* 623:63–76 [doi:10.1007/s10750-008-9648-x](https://doi.org/10.1007/s10750-008-9648-x)
240. Jimenez CR, Dejarne HE, Jimenez JU, Gaid RD (2011) Habitat characteristics, spawning, relative fecundity and larval development of *Lutraria* sp. (Bivalvia: Mactridae). *Journal of Environment and Aquatic Resources* 2:11–20 [doi:10.48031/msunjea.2011.02.02](https://doi.org/10.48031/msunjea.2011.02.02)
241. Jirkov I (2018) Three new species of *Thelepus* Leuckart, 1849 from Europe and a redescription of *T. cincinatus* (Fabricius, 1780) (Annelida, Terebellidae). *ZooKeys* 759:29–56 [PubMed doi:10.3897/zookeys.759.22981](https://pubmed.ncbi.nlm.nih.gov/doi/10.3897/zookeys.759.22981)
243. Joaquim SMD 2013. Biology and hatchery production of *Chamelea gallina*, *Spisula solida* and *Venerupis corrugata*, to support restocking and stock enhancement programs. PhD thesis, University of Algarve, 237 p.
242. Joaquim S, Matias D, Lopes B, Arnold WS, Gaspar MB (2008) The reproductive cycle of white clam *Spisula solida* (L.) (Mollusca: Bivalvia): implications for aquaculture and wild stock management. *Aquaculture* 281:43–48 [doi:10.1016/j.aquaculture.2008.05.018](https://doi.org/10.1016/j.aquaculture.2008.05.018)
244. Johansen PO (1996) Reproduction and sexual maturation of the scavenging deepwater isopod *Natanolana borealis* (Lilljeborg) from western Norway. *Sarsia* 81:297–306 [doi:10.1080/00364827.1996.10413627](https://doi.org/10.1080/00364827.1996.10413627)
246. Johnson WS, Stevens M, Watling L (2001) Reproduction and development of marine peracarideans. *Adv Mar Biol* 39:105–260 [doi:10.1016/S0065-2881\(01\)39009-0](https://doi.org/10.1016/S0065-2881(01)39009-0)
245. Johnson DD, Gray CA, Macbeth WG (2010) Reproductive biology of *Portunus pelagicus* in a south-east Australian estuary. *J Crustac Biol* 30:200–205 [doi:10.1651/08-3076.1](https://doi.org/10.1651/08-3076.1)
247. Jones DA (1970) Population densities and breeding in *Eurydice Pulchra* and *Eurydice Affinis* in Britain. *J Mar Biol Assoc UK* 50:635–655 [doi:10.1017/S0025315400004926](https://doi.org/10.1017/S0025315400004926)

249. Jones NS 1976. British Cumaceans. Arthropoda: Crustacea. Keys and notes for the identification of the species. Synopses of the British Fauna. Linnean Society of London, 62 p.
248. Jones MB, Smaldon G (1989) Aspects of the biology of a population of the cosmopolitan brittlestar *Amphipholis squamata* (Echinodermata) from the Firth of Forth, Scotland. *J Nat Hist* 23:613–625 [doi:10.1080/00222938900770341](https://doi.org/10.1080/00222938900770341)
250. Kaïm-Malka RA (1997) Biology and life cycle of *Natatoluna borealis* Lilj. 1851, a scavenging isopod from the continental slope of the Mediterranean. *Deep Sea Res I* 44:2045–2067 [doi:10.1016/S0967-0637\(97\)00050-2](https://doi.org/10.1016/S0967-0637(97)00050-2)
251. Kannevorff E (1965) Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* liljeborg from the Øresund. *Ophelia* 2:305–318 [doi:10.1080/00785326.1965.10409606](https://doi.org/10.1080/00785326.1965.10409606)
252. Kennedy JJ (1995) the courtship, pseudo-copulation behaviour and spermatophore of *Turritella communis* risso 1826 (prosobranchia: turritellidae). *J Molluscan Stud* 61:421–434 [doi:10.1093/mollus/61.4.421](https://doi.org/10.1093/mollus/61.4.421)
253. Kerr AK (1981) Aspects of the biology of *Lutraria lutraria* (L.) (Bivalvia: Macteacea). PhD thesis, University of Glasgow, 167 p.
254. Kideys AE, Nash RDM, Hartnoll RG (1993) Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. *J Mar Biol Assoc UK* 73:391–403 [doi:10.1017/S002531540003294X](https://doi.org/10.1017/S002531540003294X)
256. Kingsley-Smith PR, Richardson CA, Seed R (2003) Size-related and seasonal patterns of egg collar production in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *J Exp Mar Biol Ecol* 295:191–206 [doi:10.1016/S0022-0981\(03\)00300-9](https://doi.org/10.1016/S0022-0981(03)00300-9)
255. Kingsley-Smith PR, Richardson C, Seed R (2005) Growth and development of the veliger larvae and juveniles of *Polinices pulchellus* (Gastropoda: Naticidae). *J Mar Biol Assoc UK* 85:171–174 [doi:10.1017/S0025315405011008h](https://doi.org/10.1017/S0025315405011008h)
257. Kirkegaard J.B., 1978. Settling, growth and life span of some common polychaetes from Danish waters. *Meddelelser Danmarks Fiskeriog Havundersøgelse, New Series* 7:447–496
258. Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: Kristensen E., Kostka, J.E. (editors). *The Ecogeomorphology of Tidal Marshes*. American Geophysical Union, Washington, USA, 390 p.
259. Kruse I, Strasser M, Thiermann F (2004) The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *J Sea Res* 51:53–62 [doi:10.1016/j.seares.2003.05.004](https://doi.org/10.1016/j.seares.2003.05.004)
260. Kubo K, Shimoda K, Tamaki A (2006) Egg size and clutch size in three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan. *J Mar Biol Assoc UK* 86:103–111 [doi:10.1017/S0025315406012902](https://doi.org/10.1017/S0025315406012902)
261. Kupriyanova E, Nishi E, ten Hove HA, Rzhavsky AV (2001) Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. *Oceanogr Mar Biol Annu Rev* 39:1–101
262. Labat JP (1984) Cycle vie de *Philocheras trispinosus* (Hailstone) (Crangonidae: Decapoda) dans la région de Banyuls-sur-Mer (Méditerranée nord-occidentale). *Vie Milieu* 34:9–16
264. Lacalli TC (1980) A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. *Can Tech Rep Fish Aquat Sci* 940:1–27
263. Lacalli T (1981) Annual spawning cycles and planktonic larvae of benthic invertebrates from Passamaquoddy Bay, New Brunswick. *Can J Zool* 59:433–440 [doi:10.1139/z81-063](https://doi.org/10.1139/z81-063)
265. Lagadeuc Y, Retière C (1993) Critères d'identification rapide des stades de développement des larves de *Pectinaria koreni* (Malmgren) (Annélide polychète) de la baie de Seine (Manche). *Vie Milieu* 43:217–224
266. Lammens JJ (1967) Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Neth J Sea Res* 3:315–382 [doi:10.1016/0077-7579\(67\)90010-5](https://doi.org/10.1016/0077-7579(67)90010-5)
267. Lancaster I (1988) *Pagurus bernhardus* (L.) – An introduction to the natural history of hermit crabs. *Field Stud* 7:189–238

268. Lancaster I (1990) Reproduction and life history strategy of the hermit crab *Pagurus bernhardus*. *J Mar Biol Assoc UK* 70:129–142 [doi:10.1017/S0025315400034251](https://doi.org/10.1017/S0025315400034251)
269. Laskaridou Nott P (1980) Reproduction in *Abra alba* (Wood) and *Abra tenuis* (Montagu) (Tellinacea: Scrobiculariidae). *J Mar Biol Assoc UK* 60:465–479 [doi:10.1017/S0025315400028484](https://doi.org/10.1017/S0025315400028484)
270. Le Petillon Y, Bertrand S, Escrivà H 2020. Spawning induction and embryo micromanipulation protocols in the amphioxus *Branchiostoma lanceolatum*. In: Sprecher S.G. (editor). *Brain Development. Methods in Molecular Biology, Second Edition*. Humana Press, pp 347–359.
271. Lebour MV (1928) Studies of the Plymouth Brachyura. II. The larval stages of *Ebalia* and *Pinnotheres*. *J Mar Biol Assoc UK* 15:109–123 [doi:10.1017/S0025315400055569](https://doi.org/10.1017/S0025315400055569)
272. Lebour MV (1931) The larval stages of *Nassarius reticulatus* and *Nassarius incrassatus*. *J Mar Biol Assoc UK* 17:797–817 [doi:10.1017/S0025315400051985](https://doi.org/10.1017/S0025315400051985)
273. Lebour MV (1933) The eggs and larvae of *Turritella communis* Lamarck and *Aporrhais pes-pellicani* (L.). *J Mar Biol Assoc UK* 18:499–506 [doi:10.1017/S0025315400043836](https://doi.org/10.1017/S0025315400043836)
274. Lebour MV (1934) The eggs of early larvae of some British Turridae. *J Mar Biol Assoc UK* 19:541–554 [doi:10.1017/S0025315400046610](https://doi.org/10.1017/S0025315400046610)
275. Lebour MV (1936) Notes on the eggs and larvae of some Plymouth prosobranchs. *J Mar Biol Assoc UK* 20:547–565 [doi:10.1017/S0025315400058124](https://doi.org/10.1017/S0025315400058124)
276. Lebour MV (1938) Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *J Mar Biol Assoc UK* 23:119–144 [doi:10.1017/S002531540005400X](https://doi.org/10.1017/S002531540005400X)
277. Lebour MV (1938) The life history of *Kellia suborbicularis*. *J Mar Biol Assoc UK* 22:447–451 [doi:10.1017/S0025315400012352](https://doi.org/10.1017/S0025315400012352)
278. Lebour MV (1944) The larval stages of *Portumnus* (Crustacea Brachyura) with notes on some other genera. *J Mar Biol Assoc UK* 26:7–15 [doi:10.1017/S0025315400014429](https://doi.org/10.1017/S0025315400014429)
279. Lee CG, Huettel M, Hong JS, Reise K (2004) Carrion-feeding on the sediment surface at nocturnal low tides by the polychaete *Phyllodoce mucosa*. *Mar Biol* 145:575–583
280. Lønning S (1976) Reproductive cycle and ultrastructure of yolk development in some echinoderms from the Bergen area, western Norway. *Sarsia* 62:49–72 [doi:10.1080/00364827.1976.10411313](https://doi.org/10.1080/00364827.1976.10411313)
281. Loosanoff VL, Davis HC (1963) Rearing of bivalve mollusks. *Adv Mar Biol* 1:1–136 [doi:10.1016/S0065-2881\(08\)60257-6](https://doi.org/10.1016/S0065-2881(08)60257-6)
282. López-Jamar E, González G, Mejuto J (1987) Ecology, growth and production of *Thyasira flexuosa* (Bivalvia, Lucinacea) from Ría de la Coruña, North-West Spain. *Ophelia* 27:111–126 [doi:10.1080/00785236.1987.10422015](https://doi.org/10.1080/00785236.1987.10422015)
283. Luttikhuisen PC, Honkoop PJC, Drent J (2011) Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. *J Exp Mar Biol Ecol* 396:156–161 [doi:10.1016/j.jembe.2010.10.017](https://doi.org/10.1016/j.jembe.2010.10.017)
284. Lutz RA, Mann R, Goodsell JG, Castagna M (1982) Larval and early post-larval development of *Arctica islandica*. *J Mar Biol Assoc UK* 62:745–769 [doi:10.1017/S0025315400070314](https://doi.org/10.1017/S0025315400070314)
285. MacDonald JD, Pike RB, Williamson DI (1957) Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). *Proc Zool Soc Lond* 128:209–258 [doi:10.1111/j.1096-3642.1957.tb00265.x](https://doi.org/10.1111/j.1096-3642.1957.tb00265.x)
286. MacGinitie GE (1955) Distribution and ecology of marine invertebrates of Point Barrow, Alaska. *Smithsonian Misc Collect* 128:1–201
287. Mackay J, Gibson G (1999) The influence of nurse eggs on variable larval development in *Polydora cornuta* (Polychaeta: Spionidae). *Invertebr Reprod Dev* 35:167–176 [doi:10.1080/07924259.1999.9652383](https://doi.org/10.1080/07924259.1999.9652383)

288. Mackie ASY (1991) *Scalibregma celticum* new species (Polychaeta: Scalibregmatidae) from Europe, with a redescription of *Scalibregma inflatum* Rathke, 1843 and comments on the genus *Sclerobregma* Hartman, 1965. *Bull Mar Sci* 48:268–276
289. Macquart-Moulin C (1977) Le contrôle de l'émergence et des nages nocturnes chez les pécararides des plages de méditerranée. *Eurydice affinis* Hansen (Isopoda), *Gastrosaccus mediterraneus* Bacescu, *Gastrosaccus spinifer* (Goës) (Mysidacea). *J Exp Mar Biol Ecol* 27:61–81 [doi:10.1016/0022-0981\(77\)90054-5](https://doi.org/10.1016/0022-0981(77)90054-5)
290. Macquart-Moulin C, Kaïm-Malka R (1994) Rythme circadien endogène d'émergence et d'activité natatoire chez l'isopode profond *Cirolana borealis* lilljeborg. *Mar Behav Physiol* 24:151–164 [doi:10.1080/10236249409378888](https://doi.org/10.1080/10236249409378888)
291. Makra A, Keegan BF (1998) Microdistribution within a population of *Acrocnida brachiata* (Montagu), (Echinodermata: Ophiuroidea) in Little Killary, west coast of Ireland. *Helgol Meeresunters* 52:65–73 [doi:10.1007/BF02908737](https://doi.org/10.1007/BF02908737)
293. Manjón-Cabeza ME, Garcia-Raso JE (1998) Population structure and growth of the hermit crab *Diogenes pugilator* (Decapoda: Anomura: Diogenidae) from the northeastern Atlantic. *J Crustac Biol* 18:753–762 [doi:10.2307/1549152](https://doi.org/10.2307/1549152)
292. Manjón-Cabeza ME, García Raso JE (2000) Reproductive aspects of females of the hermit crab *Diogenes pugilator* (Crustacea: Decapoda: Anomura) from southern Spain. *J Mar Biol Assoc UK* 80:85–93 [doi:10.1017/S0025315499001599](https://doi.org/10.1017/S0025315499001599)
294. Marine Ecological Surveys Limited 2008. *Marine Macrofauna Genus Trait Handbook*. Marine Ecological Surveys Limited, Bath, UK, 184 p.
295. MarLIN 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. www.marlin.ac.uk/biotic
296. Martel A, Larrivé DH, Klein KR, Himmelman JH (1986) Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. *Mar Biol* 92:211–222 [doi:10.1007/BF00392838](https://doi.org/10.1007/BF00392838)
297. Mathivat-Lallier MH, Cazaux C (1991) Life-history of *Nephtys hombergii* in Arcachon Bay. *Estuar Coast Shelf Sci* 32:1–9 [doi:10.1016/0272-7714\(91\)90024-6](https://doi.org/10.1016/0272-7714(91)90024-6)
298. Mattos G, Cardoso RS (2012) Population dynamics of two suspension-feeding bivalves on a sheltered beach in southeastern Brazil. *Helgol Mar Res* 66:393–400 [doi:10.1007/s10152-011-0280-1](https://doi.org/10.1007/s10152-011-0280-1)
299. Mattson S (1981) Burrowing and feeding of *Goniada maculata* Ørsted (Polychaeta). *Sarsia* 66:49–51 [doi:10.1080/00364827.1981.10414519](https://doi.org/10.1080/00364827.1981.10414519)
300. Mauchline J (1971) The biology of *Schistomysis kervillei* (Crustacea, Mysidacea). *J Mar Biol Assoc UK* 51:653–658 [doi:10.1017/S0025315400015022](https://doi.org/10.1017/S0025315400015022)
301. McCurdy DG (2001) Asexual reproduction in *Pygospio elegans* Claparède (Annelida, Polychaeta) in relation to parasitism by *Lepocreadium setiferoides* (Miller and Northup) (Platyhelminthes, Trematoda). *Biol Bull* 201:45–51 [PubMed doi:10.2307/1543524](https://pubmed.ncbi.nlm.nih.gov/1543524/)
302. McHugh D (1993) A comparative study of reproduction and development in the polychaete family Terebellidae. *Biol Bull* 185:153–167 [PubMed doi:10.2307/1541996](https://pubmed.ncbi.nlm.nih.gov/1541996/)
303. McHugh D, Fong PP (2002) Do life history traits account for diversity of polychaete annelids? *Invertebr Biol* 121:325–338 [doi:10.1111/j.1744-7410.2002.tb00133.x](https://doi.org/10.1111/j.1744-7410.2002.tb00133.x)
304. McQuaid N, Briggs RP, Roberts D (2009) Fecundity of *Nephrops norvegicus* from the Irish Sea. *J Mar Biol Assoc UK* 89:1181–1188 [doi:10.1017/S0025315409000319](https://doi.org/10.1017/S0025315409000319)
305. Meadows PS, Reid A (1966) The behaviour of *Corophium volutator* (Crustacea: Amphipoda). *J Zool* 150:387–399 [doi:10.1111/j.1469-7998.1966.tb03013.x](https://doi.org/10.1111/j.1469-7998.1966.tb03013.x)
306. Méndez N, Romero J, Flos J (1997) Population dynamics and production of the polychaete *Capitella capitata* in the littoral zone of Barcelona (Spain, NW Mediterranean). *J Exp Mar Biol Ecol* 218:263–284 [doi:10.1016/S0022-0981\(97\)00078-6](https://doi.org/10.1016/S0022-0981(97)00078-6)

307. Merrill AS, Turner RD (1963) Nest building in the bivalve genera *Musculus* and *Lima*. *Veliger* 6:55–59
308. Mohamedeen H, Hartnoll RGH (1989) Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* (L.). *J Exp Mar Biol Ecol* 134:1–24 [doi:10.1016/0022-0981\(90\)90053-F](https://doi.org/10.1016/0022-0981(90)90053-F)
309. Moore HB (1936) The biology of *Echinocardium cordatum*. *J Mar Biol Assoc UK* 20:655–671 [doi:10.1017/S0025315400058239](https://doi.org/10.1017/S0025315400058239)
310. Moore PG, Cameron KS (1999) A note on a hitherto unreported association between *Photis longicaudata* (Crustacea: Amphipoda) and *Cerianthus lloydii* (Anthozoa: Hexacorallia). *J Mar Biol Assoc UK* 79:369–370 [doi:10.1017/S0025315498000447](https://doi.org/10.1017/S0025315498000447)
311. Moore PG, Wong YM (1996) Observations on the life history of *Orchomene nanus* (Coyer) (Amphipoda: Lysianassoidea) at Millport, Scotland as deduced from baited trapping. *J Exp Mar Biol Ecol* 195:53–70 [doi:10.1016/0022-0981\(95\)00094-1](https://doi.org/10.1016/0022-0981(95)00094-1)
312. Morgan TS, Rogers AD, Paterson GLJ, Hawkins LE, Shearer M (1999) Evidence for poecilogony in *Pygospio elegans* (Polychaeta: Spionidae). *Mar Ecol Prog Ser* 178:121–132 [doi:10.3354/meps178121](https://doi.org/10.3354/meps178121)
313. Mori M, Biagi F, De Ranieri S (1998) Fecundity and egg loss during incubation in Norway Lobster (*Nephrops norvegicus*) in the North Tyrrhenian Sea. *J Nat Hist* 32:1641–1650 [doi:10.3366/anh.2005.32.1.10](https://doi.org/10.3366/anh.2005.32.1.10)
314. Mortensen TH (1920) Notes on the development and the larval forms of some Scandinavian echinoderms. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 71:133–160
315. Mortimer K, Mackie ASY (2014) Morphology, feeding and behaviour of British *Magelona* (Annelida: Magelonidae), with discussions on the form and function of abdominal lateral pouches. *Mem Mus Vic* 71:177–201 [doi:10.24199/j.mmv.2014.71.15](https://doi.org/10.24199/j.mmv.2014.71.15)
316. Morton B (2011) The biology and functional morphology of *Arctica islandica* (Bivalvia: Arcticidae): a gerontophilic living fossil. *Mar Biol Res* 7:540–553 [doi:10.1080/17451000.2010.535833](https://doi.org/10.1080/17451000.2010.535833)
317. Morys C 2010. Erarbeitung von digitalen Steckbriefen der Familie Phyllodocidae (bis zu 17 Arten) bezogen auf die gesamte Ostsee (*Phyllodoce mucosa* & *Phyllodoce maculata*). BSc thesis University of Rostock.
318. Muiño R (2002) Fecundity of *Liocarcinus depurator* (Brachyura: Portunidae) in the Ría de Arousa (Galicia, north-west Spain). *J Mar Biol Assoc UK* 82:109–116 [doi:10.1017/S0025315402005222](https://doi.org/10.1017/S0025315402005222)
319. Munday BW, Keegan BF (1992) Population dynamics of *Amphiura chiajei* (Echinodermata: Ophiuroidea) in Killary Harbour, on the west coast of Ireland. *Mar Biol* 114:595–605 [doi:10.1007/BF00357256](https://doi.org/10.1007/BF00357256)
320. Mu D, Davoult D, Gentil F, Jollivet D (2006) Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. *Mol Ecol* 15:3303–3318 [PubMed doi:10.1111/j.1365-294X.2006.03000.x](https://pubmed.ncbi.nlm.nih.gov/doi/10.1111/j.1365-294X.2006.03000.x)
321. Muus K (1981) Density and growth of juvenile *Amphiura filiformis* (Ophiuroidea) in the Øresund. *Ophelia* 20:153–168 [doi:10.1080/00785236.1981.10426567](https://doi.org/10.1080/00785236.1981.10426567)
322. Myers AA, Mcgrath D (1982) Taxonomic studies on British and Irish Amphipoda. The genus *Gammaropsis*. *J Mar Biol Assoc UK* 62:93–100 [doi:10.1017/S0025315400020129](https://doi.org/10.1017/S0025315400020129)
323. Nair KKC, Anger K (1979) Experimental studies on the life cycle of *Jassa falcata* (Crustacea, Amphipoda). *Helgol Wiss Meeresunters* 32:444–452 [doi:10.1007/BF02277988](https://doi.org/10.1007/BF02277988)
324. Navarro-Barranco C, Tierno-de-Figueroa JM, Guerra-García JM, Sánchez-Tocino L, García-Gómez JC (2013) Feeding habits of amphipods (Crustacea: Malacostraca) from shallow soft bottom communities: comparison between marine caves and open habitats. *J Sea Res* 78:1–7 [doi:10.1016/j.seares.2012.12.011](https://doi.org/10.1016/j.seares.2012.12.011)
325. Newth HG (1925) The early development of *Astropecten Irregularis*, with remarks on duplicity in echinoderm larvae. *J Cell Sci* s2-69:519–554 [doi:10.1242/jcs.s2-69.275.519](https://doi.org/10.1242/jcs.s2-69.275.519)
326. Nicolaidou A (1983) Life history and productivity of *Pectinaria koreni* Malmgren (Polychaeta). *Estuar Coast Shelf Sci* 17:31–43 [doi:10.1016/0272-7714\(83\)90043-4](https://doi.org/10.1016/0272-7714(83)90043-4)
327. Nicolaisen W, Kannevorff E (1969) On the burrowing and feeding habits of the amphipods *Bathyporeia pilosa* Lindström and *Bathyporeia sarsi* Watkin. *Ophelia* 6:231–250 [doi:10.1080/00785326.1969.10409651](https://doi.org/10.1080/00785326.1969.10409651)

328. Nishihira M, Tsuchiya M, Sato M (1983) Ecological aspects of breeding behaviour and juvenile dispersal of the polychaete, *Lumbrineris latreilli* (Audouin et Milne-Edwards), at Asamushi, northern Japan. *Benthos Res* 1983:24–33 [doi:10.5179/benthos1970.1983.24](https://doi.org/10.5179/benthos1970.1983.24)
329. Noffke A, Hertweck G, Kröncke I, Wehrmann A (2009) Particle size selection and tube structure of the polychaete *Owenia fusiformis*. *Estuar Coast Shelf Sci* 81:160–168 [doi:10.1016/j.ecss.2008.10.010](https://doi.org/10.1016/j.ecss.2008.10.010)
330. Noji CIM, Noji TT (1991) Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates. *Meeresforschung* 33:235–246
331. Nozais C, Duchêne JC, Bhaud M (1997) Control of position in the water column by the larvae of *Poecilochaetus serpens*, (Polychaeta): the importance of mucus secretion. *J Exp Mar Biol Ecol* 210:91–106 [doi:10.1016/S0022-0981\(96\)02693-7](https://doi.org/10.1016/S0022-0981(96)02693-7)
332. Nozais C, Duchêne JC, Charles F, Mas S (2003) The effect of photoperiod on the timing of larval release in the Mediterranean brood-care polychaete *Eupolymnia nebulosa* (Terebellida). *J Mar Biol Assoc UK* 83:1227–1228 [doi:10.1017/S0025315403008555](https://doi.org/10.1017/S0025315403008555)
333. O'Connor BDS, McGrath D, Keegan BF (1986) Demographic equilibrium: the case of an *Amphiura* filiformis assemblage on the west coast of Ireland. *Hydrobiologia* 142:151–158 [doi:10.1007/BF00026755](https://doi.org/10.1007/BF00026755)
336. Ockelmann WK (1958) The zoology of east Greenland: marine Lamellibranchiata. *Medd Gronl* 122:1–256
334. Ockelmann KW, Muus K (1978) The biology, ecology and behaviour of the bivalve *Mysella bidentata* (Montagu). *Ophelia* 17:1–93 [doi:10.1080/00785326.1978.10425474](https://doi.org/10.1080/00785326.1978.10425474)
335. Ockelmann KW, Vahl O (1970) On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia* 8:275–294 [doi:10.1080/00785326.1970.10429564](https://doi.org/10.1080/00785326.1970.10429564)
337. Oh CW, Hartnoll RG (1999) Brood loss during incubation in *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. *J Crustac Biol* 19:467–476 [doi:10.2307/1549255](https://doi.org/10.2307/1549255)
338. Oh CW, Hartnoll RG (1999) Size at sexual maturity, reproductive output, and seasonal reproduction of *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. *J Crustac Biol* 19:252–259 [doi:10.2307/1549231](https://doi.org/10.2307/1549231)
339. Oh CW, Hartnoll RG, Nash RDM (2001) Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. *Mar Ecol Prog Ser* 214:211–223 [doi:10.3354/meps214211](https://doi.org/10.3354/meps214211)
340. Olafsson EB (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *J Anim Ecol* 55:517–526 [doi:10.2307/4735](https://doi.org/10.2307/4735)
341. Oldfield E (1961) The functional morphology of *Kellia suborbicularis* (Montagu), *Montacuta ferruginosa* (Montagu) and *M. substriata* (Montagu), (Mollusca, Lamellibranchiata). *J Molluscan Stud* 34:255–295 [doi:10.1093/oxfordjournals.mollus.a064872](https://doi.org/10.1093/oxfordjournals.mollus.a064872)
342. Oldfield E (1964) The reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). *J Molluscan Stud* 36:79–120
343. Olive PJW (1975) Reproductive biology of *Eulalia viridis* (Müller) (Polychaeta: Phyllodocidae) in the north eastern U.K. *J Mar Biol Assoc UK* 55:313–326 [doi:10.1017/S0025315400015964](https://doi.org/10.1017/S0025315400015964)
344. Olive PJW (1977) The life-history and population structure of the polychaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to the growth rings in the teeth. *J Mar Biol Assoc UK* 57:133–150 [doi:10.1017/S0025315400021299](https://doi.org/10.1017/S0025315400021299)
345. Olive PJW (1981) Control of the reproductive cycle in female *Eulalia viridis* (Polychaeta: Phyllodocidae). *J Mar Biol Assoc UK* 61:941–958 [doi:10.1017/S0025315400023079](https://doi.org/10.1017/S0025315400023079)
347. Olive PJW, Morgan PJ (1991) The reproductive cycles of four British intertidal *Nephtys* species in relation to their geographical distribution (Polychaeta: Nephtyidae). *Ophelia* 5:351–361
346. Olive PJW, Garwood PR, Bentley NG, Wright N (1981) Reproductive success, relative abundance and population structure of two species of *Nephtys* in an estuarine beach. *Mar Biol* 63:189–196 [doi:10.1007/BF00406827](https://doi.org/10.1007/BF00406827)
348. Olive PJW, Rees SW, Djunaedi A (1998) Influence of photoperiod and temperature on oocyte growth in the semelparous polychaete *Nereis* (*Neanthes*) *virens*. *Mar Ecol Prog Ser* 172:169–183 [doi:10.3354/meps172169](https://doi.org/10.3354/meps172169)

349. Oliver JS 1973. The vertical distribution of the infauna in a sublittoral sand-bottom. MSc thesis, California State University, Hayward, 60 p.
350. Olivier M, Desrosiers G, Vincent B (1992) Variations in growth and mortality of juveniles of the phyllodocid *Eteone longa* (Fabricius) on a tidal flat. *Can J Zool* 70:663–669 [doi:10.1139/z92-099](https://doi.org/10.1139/z92-099)
351. Oug E (1977) Faunal distribution close to the sediment of a shallow marine environment. *Sarsia* 63:115–121 [doi:10.1080/00364827.1977.10411329](https://doi.org/10.1080/00364827.1977.10411329)
352. Oug E (1980) On feeding and behaviour of *Ophiodromus flexuosus* (Delle Chiaje) and *Nereimyra punctata* (O.F. Müller) (Polychaeta, Hesionidae). *Ophelia* 19:175–191 [doi:10.1080/00785326.1980.10425515](https://doi.org/10.1080/00785326.1980.10425515)
353. Pandian TJ 2016. Reproduction and Development in Aquatic Invertebrates. Volume 1. Reproduction and Development in Crustacea. CRC Press, Taylor & Francis Group, 279 p.
354. Papaspyrou S, Thessalou-Legaki M, Kristensen E (2004) Impact of *Pestarella tyrrhena* on benthic metabolism in sediment microcosms enriched with seagrass and macroalgal detritus. *Mar Ecol Prog Ser* 281:165–179 [doi:10.3354/meps281165](https://doi.org/10.3354/meps281165)
355. Paula J (1988) The larval and post-larval development of Pennant's swimming crab, *Portunus latipes* (Pennant) (Brachyura, Portunidae), reared in the laboratory. *Crustaceana* 55:202–216 [doi:10.1163/156854088X00537](https://doi.org/10.1163/156854088X00537)
356. Peharda M, Ezgeta-Balić D, Radman M, Sinjkević M, Vrgoč N, Isajlović I (2012) Age, growth and population structure of *Acanthocardia tuberculata* (Bivalvia: Cardiidae) in the eastern Adriatic Sea. *Scientia Marina* 1976. *Sci Mar* 76:59–66 [doi:10.3989/scimar.03257.21A](https://doi.org/10.3989/scimar.03257.21A)
357. Perez V, Olivier F, Tremblay R, Neumeier U, Thébault J, Chauvaud L, Meziane T (2013) Trophic resources of the bivalve, *Venus verrucosa*, in the Chausey archipelago (Normandy, France) determined by stable isotopes and fatty acids. *Aquat Living Resour* 26:229–239 [doi:10.1051/alr/2013058](https://doi.org/10.1051/alr/2013058)
358. Perron FE (1978) Seasonal burrowing behavior and ecology of *Aporrhais occidentalis* (Gastropoda: Strombacea). *Biol Bull* 154:463–471 [PubMed doi:10.2307/1541072](https://pubmed.ncbi.nlm.nih.gov/1541072/)
359. Persson LE (1989) The life-cycle and productivity of *Diastylis rathkei* (cumacea: crustacea) at three near-shore localities in the Hanö Bight, Southern Baltic. *Sarsia* 74:137–144 [doi:10.1080/00364827.1989.10420532](https://doi.org/10.1080/00364827.1989.10420532)
360. Pessani D, Godino C (1991) Larval development of *Philocheras trispinosus* (Hailstone, 1835) (Decapoda: Crangonidae) reared in the laboratory. *J Crustac Biol* 11:123–137 [doi:10.2307/1548550](https://doi.org/10.2307/1548550)
361. Petch DA (1986) Selective deposit-feeding by *Lumbrineris* cf. *latreilli* (Polychaeta: Lumbrineridae), with a new method for assessing selectivity by deposit-feeding organisms. *Mar Biol* 93:443–448 [doi:10.1007/BF00401112](https://doi.org/10.1007/BF00401112)
362. Petersen ME (1999) Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* 402:107–128 [doi:10.1023/A:1003736408195](https://doi.org/10.1023/A:1003736408195)
363. Piesik Z, Obolewski K (2007) Is the bristleworm *Pygospio elegans* Claparede (Spionidae) really a deposit-feeder? *Baltic Coastal Zone* 11:5–12
364. Pike RB, Williamson DI (1959) Observations on the distribution and breeding of British hermit crabs and the stone crab (Crustacea: Diogenidae, Paguridae and Lithodidae). *Proc Zool Soc Lond* 132:551–567 [doi:10.1111/j.1469-7998.1959.tb05536.x](https://doi.org/10.1111/j.1469-7998.1959.tb05536.x)
365. Pinn EH, Ansell AD (1993) The Effect of particle size on the burying ability of the brown shrimp *Crangon crangon*. *J Mar Biol Assoc UK* 73:365–377 [doi:10.1017/S0025315400032926](https://doi.org/10.1017/S0025315400032926)
366. Pinn EH, Atkinson RJA, Rogerson A (1998) The diet of two mud-shrimps, *Calocaris macandreae* and *Upogebia stellata* (Crustacea: Decapoda: Thalassinidea). *Ophelia* 48:211–223 [doi:10.1080/00785236.1998.10426967](https://doi.org/10.1080/00785236.1998.10426967)
367. Plate S, Husemann E (1991) An alternative mode of larval development in *Scoloplos armiger* (O. F. Müller, 1776) (Polychaeta, Orbiniidae). *Helgol Meeresunters* 45:487–492 [doi:10.1007/BF02367180](https://doi.org/10.1007/BF02367180)
368. Pleijel F (1983) On feeding of *Pholoe minuta* (Fabricius, 1780) (Polychaeta: Sigalioinidae). *Sarsia* 68:21–23 [doi:10.1080/00364827.1983.10420552](https://doi.org/10.1080/00364827.1983.10420552)

369. Plyuscheva M, Martin D, Britayev T (2004) Population ecology of two sympatric polychaetes, *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae), in the White Sea. *Invertebrate Zoology* 1:65–73 [doi:10.15298/invertzool.01.1.06](https://doi.org/10.15298/invertzool.01.1.06)
370. Popović Z, Mladineo I, Ezgeta-Balić D, Trumbić Ž, Vrgoč N, Peharda M (2013) Reproductive cycle and gonad development of *Venus verrucosa* L. (Bivalvia: Veneridae) in Kaštela Bay, Adriatic Sea. *Mar Biol Res* 9:274–284 [doi:10.1080/17451000.2012.731690](https://doi.org/10.1080/17451000.2012.731690)
371. Price R, Warwick RM (1980) Temporal variations in annual production and biomass in estuarine populations of the two polychaetes, *Nephtys hombergii* and *Ampharete acutifrons*. *J Mar Biol Assoc UK* 60:481–487 [doi:10.1017/S0025315400028496](https://doi.org/10.1017/S0025315400028496)
372. Prygiel J 1987. Etude du peuplement à *Ophelia boreslis* et de l'annélide *Nephtys cirrosa* (Ehlers 1868) en Manche Orientale et en Mer du Nord Occidentale. PhD thesis, Université des Sciences et Techniques de Lille Flandres Artois, 128 p.
373. Pyefinch KA (1949) The larval stages of *Balanus crenatus* Bruguière. *J Zool* 118:916–923
374. Rabaut M 2009. Lanice conchilega, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, 354 p.
375. Radashevsky VI (2015) Spionidae (Annelida) from Lizard Island, Great Barrier Reef, Australia: the genera *Aonides*, *Dipolydora*, *Polydorella*, *Prionospio*, *Pseudopolydora*, *Rhynchospio*, and *Tripolydora*. *Zootaxa* 4019:635–694 [PubMed](https://pubmed.ncbi.nlm.nih.gov/26111646/) [doi:10.11646/zootaxa.4019.1.22](https://doi.org/10.11646/zootaxa.4019.1.22)
376. Rainbow PS (1984) An introduction to the biology of British littoral barnacles. *Field Stud* 6:1–51
- unknown 377. Rasmussen E., 1956. Faunistic and biological notes on marine invertebrates. III. The reproduction and larval development of some polychaetes from the Isefjord, with some faunistic notes. *Biologiske Meddelelser udgivet af Det Kongelige Danske Videnskabernes Selskab* 23:1–59. unknown
378. Rasmussen E (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11:1–507 [doi:10.1080/00785326.1973.10430115](https://doi.org/10.1080/00785326.1973.10430115)
379. Reddiah K (1962) The sexuality and spawning of *Manx* pectinids. *J Mar Biol Assoc UK* 42:683–703 [doi:10.1017/S0025315400054357](https://doi.org/10.1017/S0025315400054357)
380. Rees HL (1983) Pollution investigations off the north-east coast of England: community structure, growth and production of benthic macrofauna. *Mar Environ Res* 9:61–110 [doi:10.1016/0141-1136\(83\)90036-3](https://doi.org/10.1016/0141-1136(83)90036-3)
381. Remerie T, Bourgois T, Peelaers D, Vierstraete A, Vanfleteren J, Vanreusel A (2006) Phylogeographic patterns of the mysid *Mesopodopsis slabberi* (Crustacea, Mysida) in western Europe: evidence for high molecular diversity and cryptic speciation. *Mar Biol* 149:465–481 [doi:10.1007/s00227-005-0235-7](https://doi.org/10.1007/s00227-005-0235-7)
382. Richards SL (1970) Spawning and reproductive morphology of *Scolelepis squamata* (Spionidae: Polychaeta). *Can J Zool* 48:1369–1379 [doi:10.1139/z70-234](https://doi.org/10.1139/z70-234)
383. Ridgway ID, Richardson CA (2011) *Arctica islandica*: the longest lived non colonial animal known to science. *Rev Fish Biol Fish* 21:297–310 [doi:10.1007/s11160-010-9171-9](https://doi.org/10.1007/s11160-010-9171-9)
384. Rigolet C 2013. Diversité structurelle et fonctionnelle des peuplements sablo-vaseux de Bretagne sud: impact de l'expansion d'*Haploops nirae*. Thèse de doctorat, université Pierre et Marie Curie, Paris, France, 320 p.
385. Riisgård HU, Svane I (1999) Filter feeding in lancelets (*Amphioxus*), *Branchiostoma lanceolatum*. *Invertebr Biol* 118:423–432 [doi:10.2307/3227011](https://doi.org/10.2307/3227011)
386. Risk MJ, Tunnicliffe VJ (1978) Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. *J Sediment Res* 48:1287–1292
387. Rossi F, Lardicci C (2002) Role of the nutritive value of sediment in regulating population dynamics of the deposit-feeding polychaete *Streblospio shrubsolei*. *Mar Biol* 140:1129–1138 [doi:10.1007/s00227-001-0768-3](https://doi.org/10.1007/s00227-001-0768-3)
388. Rowden AA 1993. The burrowing mud shrimp *Callianassa subterranea* (Decapoda) and bioturbation in the North Sea. PhD thesis, University of Plymouth, 166 p.

389. Rowden AA, Jones MB (1994) A contribution to the biology of the burrowing mud shrimp, *Callinassa subterranea* (Decapoda: Thalassinidea). *J Mar Biol Assoc UK* 74:623–635 [doi:10.1017/S0025315400047706](https://doi.org/10.1017/S0025315400047706)
390. Rowden AA, Jones MB (1995) The burrow structure of the mud shrimp *Callinassa subterranea* (Decapoda: Thalassinidea) from the North Sea. *J Nat Hist* 29:1155–1165 [doi:10.1080/00222939500770491](https://doi.org/10.1080/00222939500770491)
391. Ruppert EE, Fox RS, Barnes RD 2004. *Invertebrate Zoology. A functional evolutionary approach*. 7th Ed. Brooks Cole, Thomson Learning learning, Inc., 990 p.
392. Russel FS 1963. *Advances in Marine Biology*. Academic Press Inc., London, 136 p.
393. Sach G (1975) Zur Fortpflanzung des Polychaeten *Anaitides mucosa*. *Mar Biol* 31:157–160 [doi:10.1007/BF00391627](https://doi.org/10.1007/BF00391627)
394. Sainte-Marie B (1990) Reproductive bionomics of some shallow-water lysianassoids in the Saint Lawrence Estuary, with a review on the fecundity of the Lysianassoidea (Crustacea, Amphipoda). *Can J Zool* 68:1639–1644 [doi:10.1139/z90-243](https://doi.org/10.1139/z90-243)
395. Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia* 223:189–227 [doi:10.1007/BF00047641](https://doi.org/10.1007/BF00047641)
396. Saleuddin ASM (1964) The gonads and reproductive cycle of *Astarte sulcata* (Da Costa) and sexuality in *A. elliptica* (Brown). *J Molluscan Stud* 36:141–148 [doi:10.1093/oxfordjournals.mollus.a064943](https://doi.org/10.1093/oxfordjournals.mollus.a064943)
397. Salman SD (1982) Observations on the larvae of north European crabs of the genus *Ebalia* (Brachyura, Leucosiidae). *Crustaceana* 42:256–269 [doi:10.1163/156854082X00326](https://doi.org/10.1163/156854082X00326)
398. San Vicente C, Sorbe JC (1993) Biologie du mysidacé suprabenthique *Schistomysis parkeri* Norman, 1892 dans la zone Sud du golfe De Gascogne (Plage D’Hendaye). *Crustaceana* 65:222–252 [doi:10.1163/156854093X00586](https://doi.org/10.1163/156854093X00586)
399. San Vicente C, Sorbe JC (2013) Comparative life-histories, population dynamics and productivity of *Schistomysis* populations (Crustacea, Mysida) in European shelf environments. *J Sea Res* 81:13–32 [doi:10.1016/j.seares.2013.03.009](https://doi.org/10.1016/j.seares.2013.03.009)
400. Sanz-Brau A, Gil-Delgado JA, Mesquita-Joanes F (2010) Seasonal variation of clutch size in the crangonid shrimp *Philocheras trispinosus* (Crustacea: Decapoda) in the Western Mediterranean (Spain). *Vie Milieu* 60:283–289
401. Sardá F (1995) A review (1967-1990) of some aspects of the life history of *Nephrops norvegicus*. *ICES Mar Sci Symp* 199:78–88
402. Sardá R, Martin D (1993) Populations of *Streblospio* (Polychaeta: Spionidae) in temperate zones: demography and production. *J Mar Biol Assoc UK* 73:769–784 [doi:10.1017/S0025315400034718](https://doi.org/10.1017/S0025315400034718)
403. Sartori AF, Domaneschi O (2005) The functional morphology of the Antarctic bivalve *Thracia meridionalis* Smith, 1885 (Anomalodesmata: Thraciidae). *J Molluscan Stud* 71:199–210 [doi:10.1093/mollus/eyi028](https://doi.org/10.1093/mollus/eyi028)
404. Sarvala J (1971) Ecology of *Harmothoe sarsi* (Malmgren) (Polychaeta, Polynoidae) in the northern Baltic area. *Ann Zool Fenn* 8:231–309
405. Sato M (1982) Ecological aspects of the development of the polychaete, *Lumbrineris latreilli* (Audouin et Milne-Edwards): significance of direct development and nonsimultaneous emergence of the young from the jelly mass. *Bulletin of the Marine Biological Station of Asamushi* 17:71–85
406. Sato M, Ozanai K (1996) Role of jelly matrix of egg masses in fertilization of the polychaete *Lumbrineris latreilli*. *Invertebr Reprod Dev* 29:185–191 [doi:10.1080/07924259.1996.9672512](https://doi.org/10.1080/07924259.1996.9672512)
407. Scaps P (2002) A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). *Hydrobiologia* 470:203–218 [doi:10.1023/A:1015681605656](https://doi.org/10.1023/A:1015681605656)
408. Schembri PJ (1981) Feeding in *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosidae). *J Exp Mar Biol Ecol* 55:1–10 [doi:10.1016/0022-0981\(81\)90088-5](https://doi.org/10.1016/0022-0981(81)90088-5)

409. Schembri PJ (1981) Substratum preferences, burrowing and righting in *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae). *Mar Behav Physiol* 8:149–161 [doi:10.1080/10236248109387011](https://doi.org/10.1080/10236248109387011)
410. Schembri PJ (1982) The biology of a population of *Ebalia tuberosa* (Crustacea: Decapoda: Leucosiidae) from the Clyde Sea Area. *J Mar Biol Assoc UK* 62:101–115 [doi:10.1017/S0025315400020130](https://doi.org/10.1017/S0025315400020130)
411. Schembri PJ (1983) Courtship and mating behaviour in *Ebalia tuberosa* (Pennant) (Decapoda, Brachyura, Leucosiidae). *Crustaceana* 45:77–81 [doi:10.1163/156854083X00217](https://doi.org/10.1163/156854083X00217)
412. Schöttler U, Grieshaber M (1988) Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. *Mar Biol* 99:215–222 [doi:10.1007/BF00391983](https://doi.org/10.1007/BF00391983)
413. Schubert A, Reise K (1986) Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. *Mar Ecol Prog Ser* 34:117–124 [doi:10.3354/meps034117](https://doi.org/10.3354/meps034117)
414. Scinto A, Benvenuto C, Cerrano C, Mori M (2007) Seasonal cycle of *Jassa marmorata* Holmes, 1903 (Amphipoda) in the Ligurian Sea (Mediterranean, Italy). *J Crustac Biol* 27:212–216 [doi:10.1651/S-2693.1](https://doi.org/10.1651/S-2693.1)
415. Scoupe C 2015. Ziemski F., in: DORIS, 16 12 2015: *Aporrhais pespelecani* (Linnaeus, 1758), <http://doris.ffessm.fr/ref/specie/2059>
416. Seed R, Brown RA (1977) A comparison of the reproductive cycles of *Modiolus modiolus* (L.), *Cerastoderma* (= *Cardium*) *edule* (L.), and *Mytilus edulis* L. in Strangford Lough, Northern Ireland. *Oecologia* 30:173–188 [PubMed doi:10.1007/BF00345419](https://pubmed.ncbi.nlm.nih.gov/doi/10.1007/BF00345419)
417. Sejr MK, Sand MK, Jensen KT, Petersen JK, Christensen PB, Rysgaard S (2002) Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). *Mar Ecol Prog Ser* 244:163–169 [doi:10.3354/meps244163](https://doi.org/10.3354/meps244163)
418. Selin NI (2007) Shell form, growth and life span of *Astarte arctica* and *A. borealis* (Mollusca: Bivalvia) from the subtidal zone of northeastern Sakhalin. *Russ J Mar Biol* 33:232–237 [doi:10.1134/S1063074007040050](https://doi.org/10.1134/S1063074007040050)
419. Sewell MA (1994) Small size, brooding, and protandry in the apodid sea cucumber *Leptosynapta clarki*. *Biol Bull* 187:112–123 [PubMed doi:10.2307/1542170](https://pubmed.ncbi.nlm.nih.gov/doi/10.2307/1542170)
420. Sewell MA, Chia FS (1994) Reproduction of the intraovarian brooding apodid *Leptosynapta clarki* (Echinodermata: Holothuroidea) in British Columbia. *Mar Biol* 121:285–300 [doi:10.1007/BF00346737](https://doi.org/10.1007/BF00346737)
421. Shafee MS (1980) Quantitative studies on the reproduction of black scallop, *Chlamys varia* (L.) from Lanveoc area, Bay of Brest. *J Exp Mar Biol Ecol* 42:171–186 [doi:10.1016/0022-0981\(80\)90174-4](https://doi.org/10.1016/0022-0981(80)90174-4)
422. Shaffer PL (1983) Population ecology of *Heteromastus filiformis* (Polychaeta: Capitellidae). *Neth J Sea Res* 17:106–125 [doi:10.1016/0077-7579\(83\)90009-1](https://doi.org/10.1016/0077-7579(83)90009-1)
423. Shalla S 2011. Identification guide to British cumaceans. NMBAQC workshop 2010, 46 p.
424. Shearer M (1977) Production and population dynamics of *Ampelisca tenuicornis* (Amphipoda) with notes on the biology of its parasite *Sphaeronella longipes* (Copepoda). *Journal of the Marine Biological Association* 57:955–968 [doi:10.1017/S0025315400026047](https://doi.org/10.1017/S0025315400026047)
425. Sigurdsson JB, Titman CW, Davies PA (1976) The dispersal of young post larval bivalve mollusks by byssus threads. *Nature* 262:386–387 [doi:10.1038/262386a0](https://doi.org/10.1038/262386a0)
426. Sikorski AV (2003) *Laonice* (Polychaeta, Spionidae) in the Arctic and the North Atlantic. *Sarsia* 88:316–345 [doi:10.1080/00364820310002551](https://doi.org/10.1080/00364820310002551)
427. Skazina M, Sofronova E, Khaitov V (2013) Paving the way for the new generations: *Astarte borealis* population dynamics in the White Sea. *Hydrobiologia* 706:35–49 [doi:10.1007/s10750-012-1271-1](https://doi.org/10.1007/s10750-012-1271-1)
428. Sola JC (1996) Population dynamics, reproduction, growth, and secondary production of the mud-snail hydrobia ulvae (Pennant). *J Exp Mar Biol Ecol* 205:49–62 [doi:10.1016/S0022-0981\(96\)02597-X](https://doi.org/10.1016/S0022-0981(96)02597-X)
429. Speybroeck J, Alsteens L, Vincx M, Degraer S (2007) Understanding the life of a sandy beach polychaete of functional importance – *Scolelepis squamata* (Polychaeta: Spionidae) on Belgian sandy beaches (northeastern Atlantic, North Sea). *Estuar Coast Shelf Sci* 74:109–118 [doi:10.1016/j.ecss.2007.04.002](https://doi.org/10.1016/j.ecss.2007.04.002)

430. Sriknshnadas B, Ramoorthi K (1981) Studies on the life-history of *Spio filicornis* (Muller 1776). *Mahasagar* 14:303–307
431. Stecher HJ (1968) Zur Organisation und Fortpflanzung von *Pisione remota* (Southern) (Polychaeta, Pisionidae). *Z Morphol Oekol Tiere* 61:347–410 [doi:10.1007/BF00573586](https://doi.org/10.1007/BF00573586)
432. Stephen AC (1928) Notes on the biology of *Tellina tenuis* da Coasta. *J Mar Biol Assoc UK* 15:683–702 [doi:10.1017/S0025315400009590](https://doi.org/10.1017/S0025315400009590)
433. Strasser M (1999) *Mya arenaria* – an ancient invader of the North Sea coast. *Helgol Meeresunters* 52:309–324 [doi:10.1007/BF02908905](https://doi.org/10.1007/BF02908905)
434. Sumida PYG 1998. Post-larval development in deep-sea echinoderms. PhD thesis, University of Southampton, Faculty of Science, School of Ocean and Earth Science, 296 p.
435. Surugiu V, Boltachova NA, Lisitskaya EV (2018) The current status of *Eunereis longissima* (Johnston, 1840) (Polychaeta: Nereididae) in the Black Sea. *Cah Biol Mar* 59:61–69
436. Tallmark B (1980) Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. *Mar Ecol Prog Ser* 3:51–62 [doi:10.3354/meps003051](https://doi.org/10.3354/meps003051)
437. Tamaki A (1987) Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. *Mar Ecol Prog Ser* 37:181–189 [doi:10.3354/meps037181](https://doi.org/10.3354/meps037181)
438. Taylor AC, Moore PG (1995) The burrows and physiological adaptations to a burrowing lifestyle of *Natatlana borealis* (Isopoda: Cirolanidae). *Mar Biol* 123:805–814 [doi:10.1007/BF00349124](https://doi.org/10.1007/BF00349124)
439. Thessalou-Legaki M (1990) Advanced larval development of *Callinassa tyrrenha* (Decapoda: Thalassinidea) and the effect of environmental factors. *J Crustac Biol* 10:659–666 [doi:10.2307/1548410](https://doi.org/10.2307/1548410)
440. Thessalou-Legaki M, Kiortsis V (1997) Estimation of the reproductive output of the burrowing shrimp *Callinassa tyrrenha*: a comparison of three different biometrical approaches. *Mar Biol* 127:435–442 [doi:10.1007/s002270050030](https://doi.org/10.1007/s002270050030)
441. Thiébaud E, Lagadeuc Y, Olivier E, Dauvin JC, Retière C (1998) Do hydrodynamic factors affect the recruitment of marine invertebrates in a macrotidal area? *Hydrobiologia* 375–376:165–176 [doi:10.1023/A:1017092518829](https://doi.org/10.1023/A:1017092518829)
442. Thiel M (1997) Reproductive biology of an epibenthic amphipod (*Dyopodos monacanthus*) with extended parental care. *J Mar Biol Assoc UK* 77:1059–1107 [doi:10.1017/S0025315400038625](https://doi.org/10.1017/S0025315400038625)
443. Thiel M, Hinojosa I 2009. Peracarida – Amphipods, Isopods, Tanaidaceans and Cumaceans. In: Häussermann V., Försterra G. (editors). *Marine Benthic Fauna of Chilean Patagonia. Nature in Focus, Puerto Montt, Chile*, pp 671–738.
444. Thompson ML, Schaffner LC (2001) Population biology and secondary production of the suspension feeding polychaete *Chaetopterus cf. variopedatus*: implications for benthic-pelagic coupling in lower Chesapeake Bay. *Limnol Oceanogr* 46:1899–1907 [doi:10.4319/lo.2001.46.8.1899](https://doi.org/10.4319/lo.2001.46.8.1899)
445. Thorarinsdottir GG, Jacobson L, Ragnarsson SA, Garcia EG, Gunnarsson K (2009) Capture efficiency and size selectivity of hydraulic clam dredges used in fishing for ocean quahogs (*Arctica islandica*): simultaneous estimation in the SELECT model. *ICES J Mar Sci* 67:345–354 [doi:10.1093/icesjms/fsp236](https://doi.org/10.1093/icesjms/fsp236)
446. Tillin HM 2016. [*Mediomastus fragilis*], [*Lumbrineris*] spp. and venerid bivalves in circalittoral coarse sand or gravel. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. DOI <https://dx.doi.org/10.17031/marlinhab.382.1>
447. Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31–45 [doi:10.3354/meps318031](https://doi.org/10.3354/meps318031)
448. Tippelt L 2010. Erarbeitung von digitalen Steckbriefen der Familie Ampeliscidae (Amphipoda) (bis 10 Arten) bezogen auf die gesamte Ostsee (*Ampelisca brevicornis* & *Ampelisca tenuicornis*). Bachelorarbeit Universität Rostock.

449. Tirado C, Salas C (1998) Reproduction and fecundity of *Donax trunculus* L., 1758 (Bivalvia: Donacidae) in the littoral of Málaga (Southern Spain). *J Shellfish Res* 17:169–176
450. Tirado C, Salas C, Márquez I (2003) Reproduction of *Venus verrucosa* L., 1758 (Bivalvia: Veneridae) in the littoral of Málaga (southern Spain). *Fish Res* 63:437–445 [doi:10.1016/S0165-7836\(03\)00106-1](https://doi.org/10.1016/S0165-7836(03)00106-1)
451. Tirelli T, Dappiano M, Maiorana G, Pessani D (2000) Intraspecific relationships of the hermit crab *Diogenes pugilator*: predation and competition. *Hydrobiologia* 439:43–48 [doi:10.1023/A:1004197518769](https://doi.org/10.1023/A:1004197518769)
452. Trevallion A (1971) Studies on *Tellina tenuis* Da Costa. III. Aspects of general biology and energy flow. *J Exp Mar Biol Ecol* 7:95–122 [doi:10.1016/0022-0981\(71\)90006-2](https://doi.org/10.1016/0022-0981(71)90006-2)
453. Trevor JH (1976) The burrowing activity of *Nephtys cirrosa* Ehlers (Annelida: Polychaeta). *J Exp Mar Biol Ecol* 24:307–319 [doi:10.1016/0022-0981\(76\)90062-9](https://doi.org/10.1016/0022-0981(76)90062-9)
454. Tuck ID, Chapman CJ, Atkinson RJA (1997) Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. I. Growth and density. *ICES J Mar Sci* 54:125–135 [doi:10.1006/jmsc.1996.0179](https://doi.org/10.1006/jmsc.1996.0179)
455. Tunberg B (1983) Growth of *Dosinia exoleta* (L.) (Bivalvia) in Raunefjorden, western Norway. *Sarsia* 68:40–45 [doi:10.1080/00364827.1983.10420556](https://doi.org/10.1080/00364827.1983.10420556)
456. Tunberg B (1983) Population structure, size distribution, and shell growth of *Dosinia lupinus* (L.) (Bivalvia) in Raunefjorden, Western Norway, with biometrical comparison to *Dosinia exoleta* (L.). *Sarsia* 68:33–40 [doi:10.1080/00364827.1983.10420555](https://doi.org/10.1080/00364827.1983.10420555)
457. Tunberg B (1984) Aspects of the population ecology of *Lucinoma borealis* (L.) (Bivalvia) in Raunefjorden, western Norway. *J Exp Mar Biol Ecol* 81:87–106 [doi:10.1016/0022-0981\(84\)90225-9](https://doi.org/10.1016/0022-0981(84)90225-9)
458. Tunberg B (1984) Population ecology of *Dosinia exoleta* (L.) (Bivalvia) in Raunefjorden, western Norway. *Sarsia* 69:159–168 [doi:10.1080/00364827.1984.10420602](https://doi.org/10.1080/00364827.1984.10420602)
459. Tunberg B (1986) Studies on the population ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassini-dea). *Estuar Coast Shelf Sci* 22:753–765 [doi:10.1016/0272-7714\(86\)90097-1](https://doi.org/10.1016/0272-7714(86)90097-1)
460. Tyler PA (1977) Seasonal variation and ecology of gametogenesis in the genus *Ophiura* (Ophiuroidea: Echinodermata) from the Bristol Channel. *J Exp Mar Biol Ecol* 30:185–197 [doi:10.1016/0022-0981\(77\)90011-9](https://doi.org/10.1016/0022-0981(77)90011-9)
461. Vader W (1969) Verspreiding en biologie van *Haustorius arenarius*, de zandvlokreeft, in Nederland (Crustacea, Amphipoda). *Zoologische Bijdragen* 2:49–58
462. Valderhaug VA (1985) Population structure and production of *Lumbrineris fragilis* (Polychaeta: Lumbrineridae) in the Oslofjord (Norway) with a note on metal content of jaws. *Mar Biol* 86:203–211 [doi:10.1007/BF00399028](https://doi.org/10.1007/BF00399028)
463. Valentin C, Anger K (1977) In-situ studies on the life cycle of *Diastylis rathkei* (Cumacea: Crustacea). *Mar Biol* 39:71–76 [doi:10.1007/BF00395596](https://doi.org/10.1007/BF00395596)
464. van der Loeff MMR, Anderson LG, Hall POJ, Iverfeldt Å, Josefson AB, Sundby B, Westerlund SFG (1984) The asphyxiation technique: an approach to distinguishing between molecular diffusion and biologically mediated transport at the sediment-water interface. *Limnol Oceanogr* 29:675–686 [doi:10.4319/lo.1984.29.4.0675](https://doi.org/10.4319/lo.1984.29.4.0675)
465. van Tomme J, Van Colen C, Degraer S, Vincx M (2012) Encounter competition partly explains the segregation of the sandy beach amphipods *Bathyporeia pilosa* and *Bathyporeia sarsi*. A mesocosm experiment. *J Exp Mar Biol Ecol* 438:118–124 [doi:10.1016/j.jembe.2012.09.012](https://doi.org/10.1016/j.jembe.2012.09.012)
466. Vevers HG (1949) The biology of *Asterias rubens* L.: growth and reproduction. *J Mar Biol Assoc UK* 28:165–187 [doi:10.1017/S0025315400055272](https://doi.org/10.1017/S0025315400055272)
467. Von Oertzen JA (1972) Cycles and rates of reproduction of six Baltic Sea bivalves of different zoogeographical origin. *Mar Biol* 14:143–149 [doi:10.1007/BF00373213](https://doi.org/10.1007/BF00373213)
468. Walting L (ed) 1991. VIIth International Colloquium on Amphipoda. Kluwer Academic, 299 p.
469. Wear RG (1974) Incubation in British decapod crustacea, and the effects of temperature on the rate and success of embryonic development. *J Mar Biol Assoc UK* 54:745–762 [doi:10.1017/S0025315400022918](https://doi.org/10.1017/S0025315400022918)

471. Webb GE (1919) The development of the species of *Upogebia* from Plymouth Sound. *J Mar Biol Assoc UK* 12:81–134 [doi:10.1017/S0025315400059920](https://doi.org/10.1017/S0025315400059920)
470. Webb CM (1986) Post-larval development of the tellinacean bivalves *Abra alba*, *Tellina fabula* and *Donax vittatus* (Mollusca: Bivalvia), with reference to the late larva. *J Mar Biol Assoc UK* 66:749–762 [doi:10.1017/S0025315400042338](https://doi.org/10.1017/S0025315400042338)
472. Webb P, Wooldridge TH (1990) Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea: Mysidacea) in Algoa Bay, southern Africa. *Mar Ecol Prog Ser* 62:73–77 [doi:10.3354/meps062073](https://doi.org/10.3354/meps062073)
473. Wells GP, Dales RP (1951) Spontaneous activity patterns in animal behaviour: the irrigation of the burrow in the polychaetes *Chaetopterus variopedatus* Renier and *Nereis diversicolor* O. F. Müller. *J Mar Biol Assoc UK* 29:661–680 [doi:10.1017/S0025315400052851](https://doi.org/10.1017/S0025315400052851)
474. Węślawski JM, Legeżyńska J (2002) Life cycles of some Arctic amphipods. *Pol Polar Res* 23:253–264
475. Widdicombe S, Austen MC, Kendall MA, Olsgard F, Schaanning MT, Dashfield SL, Needham HL (2004) Importance of bioturbators for biodiversity maintenance: indirect effects of fishing disturbance. *Mar Ecol Prog Ser* 275:1–10 [doi:10.3354/meps275001](https://doi.org/10.3354/meps275001)
477. Wikander PB (1980) Biometry and behaviour in *Abra nitida* (Müller) and *A. longicallus* (Scacchi) (Bivalvia, Tellinacea). *Sarsia* 65:255–268 [doi:10.1080/00364827.1980.10431488](https://doi.org/10.1080/00364827.1980.10431488)
476. Wikander B (1981) Quantitative aspects of deposit feeding in *Abra nitida* (Müller) and *A. longicallus* (Scacchi) (Bivalvia, Tellinacea). *Sarsia* 66:35–48 [doi:10.1080/00364827.1981.10414518](https://doi.org/10.1080/00364827.1981.10414518)
478. Wilde PAWJ, Berghuis EM, Kok A (1984) Structure and energy demand of the benthic community of the Oyster Ground, central North Sea. *Neth J Sea Res* 18:143–159 [doi:10.1016/0077-7579\(84\)90029-2](https://doi.org/10.1016/0077-7579(84)90029-2)
479. Wildish DJ (1984) Secondary production of four sublittoral, soft-sediment amphipod populations in the Bay of Fundy. *Can J Zool* 62:1027–1033 [doi:10.1139/z84-146](https://doi.org/10.1139/z84-146)
480. Wilson DP (1932) On the mitraria larva of *Owenia fusiformis* Delle Chiaje. *Philos Trans R Soc Lond B Biol Sci* 221:474–482
481. Wilson DP (1933) The larval stages of *Notomastus latericeus* Sars. *J Mar Biol Assoc UK* 18:511–518 [doi:10.1017/S002531540004385X](https://doi.org/10.1017/S002531540004385X)
482. Wilson DP (1948) The larval development of *Ophelia bicornis* Savigny. *J Mar Biol Assoc UK* 27:540–553 [doi:10.1017/S0025315400056010](https://doi.org/10.1017/S0025315400056010)
483. Wilson DP (1982) The larval development of three species of *Magelona* (Polychaeta) from localities near Plymouth. *J Mar Biol Assoc UK* 62:385–401 [doi:10.1017/S0025315400057350](https://doi.org/10.1017/S0025315400057350)
486. Wilson RS (1988) A review of *Eteone* Savigny, 1820, *Mysta*, Malmgren, 1865 and *Hypereteone* Bergström, 1914 (POLYCHAETA: PHYLLODOCIDAE). *Mem Mus Vic* 49:385–431 [doi:10.24199/j.mmv.1988.49.17](https://doi.org/10.24199/j.mmv.1988.49.17)
484. Wilson HW (1991) Sexual reproductive modes in polychaetes: classification and diversity. *Bull Mar Sci* 48:500–516
485. Wilson JG (1992) Age-specific energetics of reproduction in *Nucula turgida* (Leckenby and Marshall) a bivalve with lecithotrophic larval development. *Invertebr Reprod Dev* 22:275–279 [doi:10.1080/07924259.1992.9672280](https://doi.org/10.1080/07924259.1992.9672280)
487. Wilson WH Jr, Ruff RE 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) sandworm and bloodworm. U.S. Fish. Wildl. Serv. Biological Report 82 (11.80). U.S. Army Corps of Engineers, TR EL-82-4, 23 p.
488. Witbaard R, Duineveld GCA, Amaro T, Bergman MJN (2005) Growth trends in three bivalve species indicate climate forcing on the benthic ecosystem in the southeastern North Sea. *Clim Res* 30:29–38 [doi:10.3354/cr030029](https://doi.org/10.3354/cr030029)
489. Wittmann KJ (1984) Ecophysiology of Marsupial Development and Reproduction in Mysidacea (Crustacea). *Oceanogr Mar Biol Annu Rev* 22:417–458

490. Wong YM, Moore PG (1995) Biology of feeding in the scavenging isopod *Natanolana borealis* (Isopoda: Cirolanidae). *Ophelia* 43:181–196 [doi:10.1080_00785326.1995.10429830](https://doi.org/10.1080_00785326.1995.10429830)
491. Woodson Lehane JR 2014. Applications of quantitative methods and chaos theory in ichnology for analysis of invertebrate behavior and evolution. PhD thesis, University of Utah, 433 p.
492. Word JQ 1980. Classification of benthic invertebrates into infaunal trophic index feeding groups. In: Coastal Water Research Project Biennial Report 1979–1980. SCCWRP, Long Beach, California, USA, pp 103–121.
493. Yoda M, Aoki M (2002) Comparative study of benthic and pelagic populations of *Bodotria similis* (Cuma-cea) from Izu Peninsula, southern Japan. *J Crustac Biol* 22:543–552 [doi:10.1163_20021975-99990266](https://doi.org/10.1163_20021975-99990266)
495. Yonge CM (1946) On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*. *J Mar Biol Assoc UK* 26:358–376 [PubMed doi:10.1017_S0025315400012182](https://pubmed.ncbi.nlm.nih.gov/doi/10.1017_S0025315400012182)
494. Yonge CM (1951) Observations on *Sphenia binghami* Turton. *J Mar Biol Assoc UK* 30:387–392 [doi:10.1017_S0025315400012856](https://doi.org/10.1017_S0025315400012856)
496. Yonow H (1996) Gametogenesis, egg production and development in *Acteon tornatilis*. *Malacol Rev* (Supplement 6):31–52
497. Yonow N, Ryland JS 1992. Growth and life history parameters in *Acteon tornatilis* (L.) (Opisthobranchia: Cephalaspidea). *Marine Eutrophication and Population Dynamics*. Proc. 25th EMBS (eds G Colombo et al.), pp 271 – 276.
498. Yu OH, Soh HY, Suh HL (2002) Life history and reproduction of *Synchelidium lenorostralum* (Amphipoda, Oedicerotidae) in a temperate sandy shore, southern Korea. *J Crustac Biol* 22:126–134
499. Zajac RN (1991) Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Mar Ecol Prog Ser* 77:197–206 [doi:10.3354_meps077197](https://doi.org/10.3354_meps077197)
500. Zajac RN, Whitlatch RB (1988) Population ecology of the polychaete *Nephtys incisa* in Long Island Sound and the effects of disturbance. *Estuaries* 11:117–133 [doi:10.2307_1351999](https://doi.org/10.2307_1351999)
501. Zajac RN, Whitlatch RB (1989) Natural and disturbance-induced demographic variation in an infaunal polychaete, *Nephtys incisa*. *Mar Ecol Prog Ser* 57:89–102 [doi:10.3354_meps057089](https://doi.org/10.3354_meps057089)
502. Zühlke R, Blome D, van Bernem KH, Dittmann S (1998) Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. *Senckenb Marit* 29:131–138 [doi:10.1007_BF03043951](https://doi.org/10.1007_BF03043951)

Table S4. Pearson’s *r* correlations of all individual habitat and trait modalities (binary variables) with RLQ axes. Empty cell: absence of modality due to absence of habitat characteristic or representative taxon

Data	Variable	Whole area				Low dynamics				High dynamics				
		Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2		
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	
Habitat	Depth – Very shallow	0.051	0.00802	0.013	0.48950					0.017	0.57311	-0.053	0.04018	
	Depth – Shallow	0.035	0.19352	0.070	0.00987					-0.112	0.01525	-0.078	0.08843	
	Depth – Intermediate	0.072	0.00987	-0.031	0.25222	0.025	0.25311	-0.023	0.17245	0.074	0.02858	0.051	0.11620	
	Depth – Deep	-0.023	0.14345	-0.023	0.11748	0.032	0.14727	-0.045	0.02120	0.006	0.83791	0.052	0.02338	
	Depth – Very deep	-0.090	0.00987	0.003	0.94969	-0.039	0.06636	0.051	0.01490	0.040	0.12666	-0.026	0.32804	
	Current speed – Very low	-0.084	0.00994	-0.038	0.25158	0.017	0.43355	0.055	0.00742	-0.029	0.36724	0.091	0.01074	
	Current speed – Low	-0.025	0.10578	0.030	0.04133	-0.027	0.22215	-0.050	0.00742	-0.077	0.00346	0.000	0.99498	
	Current speed – Intermediate	0.027	0.13085	0.013	0.47672	0.020	0.40213	-0.016	0.38451	-0.050	0.04070	-0.009	0.74665	
	Current speed – High	0.083	0.00802	-0.004	0.93443					0.099	0.00346	-0.042	0.20003	
	Current speed – Very high	0.055	0.05115	0.012	0.72285					0.060	0.10318	-0.046	0.20003	
	Wave – Very low	-0.074	0.01097	0.004	0.93443	-0.035	0.10788	0.039	0.05632					
	Wave – Low	-0.067	0.00987	-0.001	0.97900	0.016	0.44125	-0.036	0.04670	-0.016	0.58202	0.030	0.12666	
	Wave – Intermediate	0.048	0.01347	-0.035	0.07796	0.043	0.01305	-0.005	0.77231	0.052	0.06808	0.033	0.21343	
	Wave – High	0.057	0.00987	-0.022	0.32853					0.042	0.08790	0.030	0.17414	
	Wave – Very high	0.050	0.06891	0.056	0.04435					-0.088	0.04018	-0.073	0.08645	
	Stratification – FI	0.044	0.03390	-0.002	0.94969	-0.018	0.43355	-0.022	0.22215	0.036	0.14764	-0.007	0.76945	
	Stratification – PM	0.031	0.11349	0.041	0.03434					-0.037	0.12666	-0.048	0.05277	
	Stratification – IS	0.038	0.01404	-0.019	0.19156	0.061	0.00220	-0.046	0.00742	0.015	0.57541	0.017	0.49515	
	Stratification – SS	-0.027	0.08202	-0.013	0.36994	-0.001	0.97893	0.025	0.14727					
	Stratification – TR	-0.078	0.00802	0.004	0.93443	-0.047	0.02489	0.036	0.02802	-0.030	0.23304	0.032	0.14095	
	Sediment – Muddy	-0.086	0.00802	0.029	0.33690	-0.094	0.00020	-0.012	0.61454	-0.018	0.49515	0.053	0.00346	
	Sediment – Sandy	0.056	0.00802	-0.041	0.03646	0.108	0.00020	0.016	0.53211	-0.014	0.61262	-0.009	0.69833	
	Sediment – Mixed	-0.020	0.19156	0.017	0.26936	-0.026	0.22215	-0.020	0.28070					
	Sediment – Coarse	0.034	0.05115	0.017	0.32853	-0.019	0.43355	0.004	0.74804	0.023	0.37777	-0.016	0.52155	
	Particulate organic matter	-0.082	0.00987	-0.013	0.72631	-0.044	0.03325	0.032	0.06571	0.005	0.85834	0.040	0.11620	
	Particulate organic carbon	-0.106	0.00817	0.046	0.24074	-0.093	0.00027	-0.040	0.09159	-0.094	0.01074	0.006	0.85834	
	Primary productivity	0.080	0.00802	0.034	0.22220	-0.010	0.62008	-0.066	0.00160	0.055	0.04018	-0.081	0.00346	
	Traits	Body mass – Very small	0.074	0.01778	-0.001	0.97011	0.023	0.46644	-0.001	0.97572	0.033	0.23519	-0.031	0.26553
		Body mass – Small	-0.020	0.69516	-0.010	0.85489	-0.016	0.66697	-0.023	0.46644	0.036	0.18588	0.009	0.78128
		Body mass – Intermediate	0.003	0.97011	0.001	0.97011	0.019	0.56490	-0.010	0.81548	-0.017	0.60017	0.021	0.50120
		Body mass – Large	-0.047	0.17891	-0.011	0.81500	-0.013	0.71324	0.028	0.46048	-0.015	0.62088	0.039	0.16462
		Body mass – Very large	-0.020	0.69516	0.034	0.37655	-0.019	0.56490	0.023	0.46644	-0.095	0.00062	-0.070	0.00928
		Motility – Sessile	-0.058	0.09804	-0.009	0.86171	-0.018	0.59107	0.035	0.32072	-0.013	0.75252	0.018	0.61465
		Motility – Tubicolous	-0.048	0.17488	0.050	0.15203	-0.063	0.00733	-0.025	0.46644	-0.045	0.10974	-0.040	0.12972
		Motility – Crawler	-0.046	0.18139	-0.019	0.69516	0.008	0.85613	0.015	0.69134	-0.085	0.00114	0.052	0.05987
		Motility – Crawler–Swimmer	0.104	0.00114	-0.016	0.75347	0.051	0.03555	-0.007	0.89347	0.128	0.00019	-0.025	0.38443
		Burrowing depth – Surficial	0.068	0.03534	-0.011	0.81325	0.066	0.00418	0.003	0.95029	0.091	0.00062	0.019	0.52996
		Burrowing depth – Shallow	-0.083	0.00557	-0.003	0.97011	-0.028	0.45913	0.005	0.90764	-0.063	0.01969	0.011	0.71310
		Burrowing depth – Intermediate	0.055	0.10700	0.021	0.66997	-0.016	0.65451	0.002	0.96862	-0.038	0.16462	-0.044	0.10476
		Burrowing depth – Deep	-0.055	0.10983	-0.010	0.85265	-0.023	0.46644	-0.013	0.72096	0.021	0.43698	0.027	0.38443
		Feeding type – De	0.032	0.41769	0.002	0.97011	-0.008	0.86814	-0.020	0.54825	0.070	0.00536	-0.017	0.55887
		Feeding type – SuDe	-0.042	0.24712	0.026	0.54970	-0.024	0.46644	-0.005	0.90764	-0.067	0.01969	-0.028	0.29667
		Feeding type – Su	-0.025	0.59092	-0.035	0.37655	0.012	0.77218	0.024	0.46644	-0.052	0.06669	0.046	0.09624
		Feeding type – CaSc	-0.009	0.86286	-0.001	0.97011	0.017	0.63954	0.005	0.90764	0.014	0.60017	0.005	0.89745
		Feeding type – Om	0.042	0.22824	0.011	0.81325	0.005	0.90764	0.000	0.99876	0.015	0.59179	0.005	0.90032
Life span – <1		0.045	0.18471	-0.002	0.97011	0.013	0.71324	-0.045	0.07098	0.054	0.04739	0.003	0.93830	
Life span – 1–3		0.017	0.74761	0.001	0.97011	-0.000	0.99876	0.023	0.46644	0.000	0.98294	-0.047	0.08205	
Life span – 3–10		-0.033	0.39275	0.026	0.54970	-0.022	0.46644	0.002	0.97572	-0.064	0.01912	-0.008	0.76699	
Life span – >10		-0.048	0.17488	-0.041	0.25167	0.014	0.70399	0.026	0.46644	0.014	0.60017	0.101	0.00033	
Age at maturity – <1		0.073	0.02332	0.015	0.76167	0.008	0.87224	-0.034	0.28255	0.047	0.08205	-0.056	0.04169	
Age at maturity – 1–3		-0.052	0.13030	0.001	0.97011	-0.005	0.90764	0.034	0.28255	-0.062	0.01969	0.000	0.99502	
Age at maturity – >3		-0.034	0.38853	-0.025	0.58538	-0.004	0.90764	-0.000	0.99876	0.023	0.40804	0.099	0.00051	

Table S4. Continued

Data	Variable	Whole area				Low dynamics				High dynamics			
		Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
	Reproductive frequency – Seasonal	-0.125	0.00057	-0.005	0.93112	-0.064	0.00608	0.020	0.55342	-0.076	0.00306	0.051	0.06337
	Reproductive frequency – Continuous	0.125	0.00057	0.005	0.93112	0.064	0.00608	-0.020	0.55342	0.076	0.00306	-0.051	0.06337
	Annual fecundity – <10 ²	0.065	0.05016	-0.028	0.52896	0.055	0.02445	0.007	0.89347	0.094	0.00019	0.013	0.68151
	Annual fecundity – 10 ² –10 ³	0.021	0.69516	0.020	0.69516	-0.053	0.02668	-0.018	0.59881	0.021	0.43804	-0.050	0.06337
	Annual fecundity – 10 ³ –10 ⁴	-0.028	0.54544	-0.012	0.81325	-0.006	0.90764	-0.010	0.81548	0.004	0.88487	0.023	0.44016
	Annual fecundity – 10 ⁴ –10 ⁵	-0.043	0.23537	0.013	0.77043	0.025	0.46644	-0.012	0.72475	-0.111	0.00019	0.034	0.24708
	Annual fecundity – >10 ⁵	-0.017	0.75347	0.002	0.97011	-0.016	0.66078	0.042	0.11836	0.004	0.88487	-0.013	0.61465
	Fertilization – Broadcasting	-0.064	0.05164	-0.022	0.65950	0.004	0.90911	0.024	0.46644	-0.046	0.09624	0.030	0.29124
	Fertilization – Spermcasting	-0.031	0.46782	0.033	0.39111	-0.059	0.01724	-0.009	0.83131	-0.044	0.12104	-0.023	0.40819
	Fertilization – Pairing	0.088	0.00475	0.001	0.97011	0.038	0.18500	-0.019	0.56490	0.080	0.00207	-0.015	0.60017
	Offspring type – Egg	-0.084	0.00557	-0.019	0.69516	-0.032	0.32386	0.014	0.70399	-0.027	0.35009	0.048	0.08205
	Offspring type – Larva	0.011	0.81325	0.047	0.17488	-0.009	0.83131	-0.025	0.46644	-0.094	0.00066	-0.040	0.12972
	Offspring type – Juvenile	0.089	0.00475	-0.018	0.74065	0.047	0.06244	0.005	0.90764	0.104	0.00019	-0.023	0.42190
	Offspring size – <0.1	-0.057	0.10282	-0.003	0.97011	-0.004	0.90764	0.027	0.46644	-0.098	0.00051	0.004	0.90563
	Offspring size – 0.1–0.5	-0.014	0.76167	0.001	0.97011	-0.030	0.37782	-0.022	0.46644	0.008	0.79601	0.028	0.31953
	Offspring size – 0.5–1.5	0.072	0.02584	-0.016	0.76167	0.080	0.00228	-0.019	0.56490	0.060	0.02478	-0.004	0.87727
	Offspring size – >1.5	0.025	0.56548	0.014	0.76167	-0.014	0.70399	0.013	0.72096	0.040	0.13213	-0.042	0.10974
	Off. protection – None	-0.054	0.10983	-0.034	0.38277	-0.005	0.90764	0.023	0.46644	-0.029	0.30184	0.050	0.06669
	Off. protection – Jelly mass	-0.056	0.10983	0.045	0.18471	-0.082	0.00228	-0.023	0.46644	-0.033	0.29667	-0.038	0.14095
	Off. protection – Collar mass	-0.015	0.76167	-0.010	0.85489	0.029	0.45913	0.000	0.99876	0.041	0.10974	0.025	0.44016
	Off. protection – Bearing/Brooding	0.085	0.00557	0.020	0.69516	0.032	0.32386	-0.014	0.70399	0.027	0.35229	-0.048	0.08205
	Off. development – Internal	0.090	0.00475	-0.019	0.71544	0.049	0.05121	0.003	0.93640	0.104	0.00019	-0.022	0.42515
	Off. development – Mixed lecithotrophic	0.060	0.07378	0.044	0.20163	0.030	0.45913	-0.025	0.46644	-0.046	0.12104	-0.043	0.09624
	Off. development – Mixed planktotrophic	-0.015	0.76167	0.040	0.25167	-0.028	0.45913	-0.023	0.46644	-0.040	0.15344	-0.033	0.22503
	Off. development – Lecithotrophic	-0.065	0.05016	-0.010	0.84783	-0.046	0.07098	-0.002	0.96862	0.014	0.60017	0.026	0.39914
	Off. development – Planktotrophic	-0.037	0.33375	-0.020	0.69516	0.009	0.83131	0.022	0.46644	-0.055	0.04698	0.040	0.14095
	Off. benthic stage duration – Null	-0.054	0.10983	-0.028	0.52365	0.003	0.95625	0.015	0.70399	-0.062	0.01969	0.048	0.08295
	Off. benthic stage duration – <15	-0.005	0.97011	0.063	0.05164	-0.069	0.00456	-0.006	0.89347	-0.034	0.24488	-0.084	0.00114
	Off. benthic stage duration – >15	0.060	0.07404	-0.012	0.81325	0.043	0.08935	-0.011	0.78331	0.086	0.00096	0.003	0.91248
	Off. pelagic stage duration – Null	0.047	0.17488	-0.016	0.75347	0.009	0.83131	0.010	0.81548	0.114	0.00019	-0.010	0.71310
	Off. pelagic stage duration – <15	-0.015	0.76167	0.014	0.76167	-0.001	0.97572	-0.023	0.46644	-0.052	0.07860	-0.020	0.45300
	Off. pelagic stage duration – >15	-0.034	0.38588	0.006	0.92891	-0.008	0.86814	0.006	0.89347	-0.074	0.00295	0.022	0.43804

Table S5. Spatial predictions of RLQ patterns by Moran’s Eigenvector Maps (MEM) according to the forward selection procedure of Blanchet et al. (2008). For large-scale and low dynamics patterns, since only the first RLQ axis was significantly correlated to both habitat descriptors and biological traits, the modeling procedure was a multiple regression. For the high dynamics pattern, computations were performed through redundancy analysis of the two first RLQ axes. Fisher’s F significance was tested by 99999 random permutations of the sampling stations

RLQ pattern	Selected MEM	R^2	Cumulative R^2	Adjusted R^2	F	p
Whole area	MEM1	0.64	0.64	0.63	176.77	< 0.0001
	MEM4	0.04	0.67	0.67	11.63	0.0011
	MEM5	0.03	0.71	0.70	10.62	0.0015
	MEM8	0.03	0.73	0.72	9.45	0.0026
	MEM2	0.02	0.75	0.74	8.67	0.0042
	MEM12	0.02	0.77	0.76	8.28	0.0047
	MEM7	0.02	0.79	0.78	8.41	0.0044
	MEM6	0.02	0.81	0.79	7.45	0.0072
	MEM24	0.01	0.82	0.80	7.55	0.0071
	MEM33	0.01	0.83	0.82	6.95	0.0093
	MEM15	0.01	0.85	0.83	7.23	0.0088
	MEM9	0.01	0.86	0.84	7.72	0.0069
	MEM44	0.01	0.87	0.85	7.04	0.0098
	MEM23	0.01	0.88	0.86	6.04	0.0162
	MEM21	0.01	0.88	0.86	5.18	0.0257
	MEM20	0.01	0.89	0.87	5.32	0.0235
	MEM30	0.01	0.90	0.88	5.43	0.0231
	MEM96	0.01	0.90	0.88	4.46	0.0380
	MEM18	< 0.01	0.91	0.89	4.39	0.0406
	MEM3	< 0.01	0.91	0.89	4.16	0.0449
MEM97	< 0.01	0.92	0.89	4.07	0.0465	
MEM89	< 0.01	0.92	0.90	4.05	0.0475	
MEM84	< 0.01	0.92	0.90	4.19	0.0429	
MEM38	< 0.01	0.93	0.91	4.10	0.0464	
MEM13	< 0.01	0.93	0.91	4.12	0.0452	
MEM40	< 0.01	0.94	0.91	3.98	0.0496	
Low dynamics	MEM1	0.30	0.30	0.28	16.44	0.0004
	MEM4	0.12	0.41	0.38	7.58	0.0094
	MEM33	0.07	0.48	0.44	4.94	0.0340
	MEM6	0.07	0.55	0.50	5.40	0.0267
	MEM13	0.06	0.61	0.55	4.98	0.0335
	MEM3	0.05	0.65	0.59	4.44	0.0428
	MEM14	0.04	0.69	0.63	4.24	0.0455
	MEM11	0.04	0.73	0.66	4.70	0.0403
High dynamics	MEM5	0.15	0.15	0.13	10.48	0.0002
	MEM3	0.13	0.28	0.26	11.02	0.0001
	MEM1	0.09	0.37	0.34	8.22	0.0009
	MEM13	0.06	0.43	0.39	6.11	0.0037
	MEM8	0.06	0.49	0.45	6.47	0.0022
	MEM7	0.05	0.54	0.49	5.71	0.0050
	MEM19	0.04	0.58	0.53	5.56	0.0059
	MEM20	0.04	0.62	0.56	5.43	0.0069
	MEM2	0.04	0.66	0.60	5.38	0.0059
	MEM40	0.02	0.68	0.62	3.86	0.0253
	MEM14	0.02	0.70	0.63	3.21	0.0426

Table S6. Growth rate data used in Figure S7

Taxon	Growth rate (cm yr ⁻¹)	Reference	Taxon	Growth rate (cm yr ⁻¹)	Reference
<i>Abra alba</i>	1.5	Dauvin and Gentil 1989	<i>Heteromastus filiformis</i>	20.0	Can et al. 2009
<i>Abra prismatica</i>	1.5	Dauvin and Gentil 1989	<i>Hiatella arctica</i>	0.1	Sejr et al. 2002
<i>Abra tenuis</i>	0.4	Dekker and Beukema 1993	<i>Idotea linearis</i>	8.2	Franke and Beermann 2014
<i>Acanthocardia</i> sp.	0.8	Peharda 2012	<i>Iphinoe trispinosa</i>	1.8	Corey 1969
<i>Acteon tornatilis</i>	1.2	Yonow and Ryland 1992	<i>Jassa marmorata</i>	3.3	Clancy 1997
<i>Alitta virens</i>	5.0	Kristensen 1984	<i>Kurtiella bidentata</i>	0.1	Ockelmann and Muus 1978
<i>Ampelisca brevicornis</i>	4.0	Dauvin 1988	<i>Lanice conchilega</i>	5.3	Van Hoey 2006
<i>Ampelisca macrocephala</i>	1.6	Kannevorff 1965	<i>Lepidonotus squamatus</i>	4.4	Plyuscheva et al. 2004
<i>Ampelisca tenuicornis</i>	1.3	Dauvin 1988	<i>Limecola balthica</i>	0.3	Cardoso et al. 2007
<i>Ampharete</i> sp.	2.5	Price and Warwick 1980	<i>Macomangulus tenuis</i>	0.4	Dekker and Beukema 1999
<i>Amphipholis squamata</i>	3.6	Emson and Whitfield 1989	<i>Magelona mirabilis</i>	4.0	Rees 1983
<i>Amphiura filiformis</i>	2.5	Sköld et al. 1994	<i>Malacoceros fuliginosus</i>	5.0	Gudmundsson 1985
<i>Arctica islandica</i>	0.2	Ridgway and Richardson 2011	<i>Mesopodopsis slabberi</i>	1.0	Delgado et al. 1997
<i>Astarte</i> sp.	0.6	Selin 2007	<i>Modiolus</i> sp.	0.2	Anwar et al. 1990
<i>Asterias rubens</i>	2.4	Nichols and Barker 1984	<i>Mya arenaria</i>	0.8	Brousseau 1979
<i>Astropecten</i> sp.	2.7	Freeman et al. 2001	<i>Mya truncata</i>	0.4	Amaro et al. 2003
<i>Balanus crenatus</i>	1.9	Barnes and Powell 1953	<i>Mymachlamys</i>	0.8	Conan and Shafee 1978
<i>Branchiostoma lanceolatum</i>	0.8	Desdevises et al. 2011	<i>Mytilus edulis</i>	0.8	Bayne and Worrall 1980
<i>Buccinum undatum</i>	0.9	Kideys 1996	<i>Nassarius reticulatus</i>	0.6	Barroso et al. 2005
<i>Callianassa subterranea</i>	3.0	Rowden and Jones 1994	<i>Nephrops norvegicus</i>	1.5	Tuck et al. 1997
<i>Capitella capitata</i>	3.0	Warren 1976	<i>Nephtys</i> sp.	3.2	Kirkegaard 1970
<i>Carcinus maenas</i>	4.5	Yamada et al. 2005	<i>Notomastus latericeus</i>	3.0	Giangrande and Fraschetti 1993
<i>Chaetopterus variopedatus</i>	20.0	Enders 1909	<i>Nucula nitidosa</i>	0.1	Rees 1983
<i>Chamelea striatula</i>	0.3	Guillou and Sauriau 1985	<i>Ophiura</i> sp.	2.5	Gage 1990
<i>Corbula gibba</i>	0.6	Jensen 1990	<i>Pagurus bernhardus</i>	3.0	Lancaster 1990
<i>Corophium volutator</i>	2.0	McLusky 1967	<i>Peringia ulvae</i>	0.3	Sola 1996
<i>Crangon crangon</i>	0.6	Henderson and Holmes 1987	<i>Philocheras trispinosus</i>	3.0	Labat 1984
<i>Diastylis rathkei</i>	1.2	Valentin and Anger 1977	<i>Pholoe minuta</i>	0.1	Heffernan 1985
<i>Diogenes pugilator</i>	2.3	Manjón-Cabeza and García Raso 1998	<i>Phoronis</i> sp.	5.0	Emig 1982
<i>Donax vittatus</i>	0.5	Ansell 1972	<i>Polydora</i> sp.	6.0	Gudmundsson 1985
<i>Dosinia exoleta</i>	0.4	Tunberg 1983	<i>Pontocrates altamarinus</i>	0.9	Beare and Moore 1998
<i>Dosinia lupinus</i>	0.3	Tunberg 1983	<i>Pontocrates arenarius</i>	0.6	Beare and Moore 1998
<i>Dyopedos monacantha</i>	1.4	Thiel 1998	<i>Psammechinus miliaris</i>	0.2	Jensen 1969
<i>Echinocardium</i> sp.	0.6	Buchanan 1966	<i>Pygospio elegans</i>	2.3	Gudmundsson 1985
<i>Ensis ensis</i>	1.9	Henderson and Richardson 1994	<i>Sphenia binghami</i>	0.1	George and Warwick 1985
<i>Ensis leei</i>	4.0	Swennen et al. 1985	<i>Spio martinensis</i>	5.0	Gudmundsson 1985
<i>Ensis siliqua</i>	2.1	Henderson and Richardson 1994	<i>Spiophanes bombyx</i>	4.0	Rees 1983
<i>Eupolyornia nebulosa</i>	4.9	Bhaud 1988	<i>Spisula solida</i>	0.7	Gaspar et al. 1995
<i>Eurydice pulchra</i>	0.5	Fish 1970	<i>Spisula subtruncata</i>	0.6	Cardoso et al. 2007
<i>Fabulina fabula</i>	1.2	Withers 1977	<i>Streblospio shrubsolii</i>	3.4	Krevrekidis 2005
<i>Gammaridae</i>	3.5	Neuparth et al. 2002	<i>Thyasira flexuosa</i>	0.2	López-Jamar et al. 1987
<i>Glycera</i> sp.	7.5	Ockelmann and Vahl 1970	<i>Venus</i> sp.	0.4	Arneri et al. 1998
<i>Harmothoe</i> sp.	8.4	Plyuscheva et al. 2004	<i>Westwoodilla caecula</i>	0.6	Beare and Moore 1998
<i>Hediste diversicolor</i>	4.0	Kristensen 1984			

REFERENCES

- Amaro T, Duineveld G, Bergman M, Witbaard R (2003) Growth variations in the bivalve *Mya truncata*: a tool to trace changes in the Frisian Front macrofauna (southern North Sea)? *Helgol Mar Res* 57:132–138 [doi:10.1007/s10152-003-0150-6](https://doi.org/10.1007/s10152-003-0150-6)
- Ansell AD (1972) Distribution, growth and seasonal changes in biochemical composition for the bivalve *Donax vittatus* (da Costa) from Kames Bay, Millport. *J Exp Mar Biol Ecol* 10:137–150 [doi:10.1016/0022-0981\(72\)90099-8](https://doi.org/10.1016/0022-0981(72)90099-8)
- Anwar NA, Richardson CA, Seed R (1990) Age determination, growth rate and population structure of the horse mussel *Modiolus modiolus*. *J Mar Biol Assoc UK* 70:441–457 [doi:10.1017/S0025315400035529](https://doi.org/10.1017/S0025315400035529)
- Arneri E, Giannetti G, Antolini B (1998) Age determination and growth of *Venus verrucosa* L. (Bivalvia: Veneridae) in the southern Adriatic and the Aegean Sea. *Fish Res* 38:193–198 [doi:10.1016/S0165-7836\(98\)00146-5](https://doi.org/10.1016/S0165-7836(98)00146-5)
- Barnes H, Powell HT (1953) The growth of *Balanus balanoides* (L.) and *B. crenatus* Brug. under varying conditions of submersion. *J Mar Biol Assoc UK* 32:107–127 [doi:10.1017/S0025315400011450](https://doi.org/10.1017/S0025315400011450)

- Barroso CM, Moreira MH, Richardson CA (2005) Age and growth of *Nassarius reticulatus* in the Ria de Aveiro, north-west Portugal. *J Mar Biol Assoc UK* 85:151–156 [doi:10.1017/S0025315405010970h](https://doi.org/10.1017/S0025315405010970h)
- Bayne BL, Worrall CM (1980) Growth and production of mussels *Mytilus edulis* from two populations. *Mar Ecol Prog Ser* 3:317–328 [doi:10.3354/meps003317](https://doi.org/10.3354/meps003317)
- Beare DJ, Moore PG (1998) Aspects of the life histories of *Perioculodes longimanus*, *Pontocrates arcticus* and *Synchelidium maculatum* (Crustacea: Amphipoda) at Millport, Scotland. *J Mar Biol Assoc UK* 78:193–209 [doi:10.1017/S0025315400040029](https://doi.org/10.1017/S0025315400040029)
- Bhaud M (1988) Influence of temperature and food supply on development of *Eupolyornia nebulosa* (Montagu, 1818) (Polychaeta: Terebellidae). *J Exp Mar Biol Ecol* 118:103–113 [doi:10.1016/0022-0981\(88\)90234-1](https://doi.org/10.1016/0022-0981(88)90234-1)
- Brousseau DJ (1979) Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Mar Biol* 51:221–227 [doi:10.1007/BF00386801](https://doi.org/10.1007/BF00386801)
- Buchanan JB (1966) The biology of *Echinocardium cordatum* (Echinodermata: Spatangoidea) from different habitats. *J Mar Biol Assoc UK* 46:97–114 [doi:10.1017/S0025315400017574](https://doi.org/10.1017/S0025315400017574)
- Can E, Kevrekidis T, Cihangir B (2009) Factors affecting monthly variation in population density of the capitellid polychaete *Heteromastus filiformis* in a hyperhaline Mediterranean coastal lagoon. *Transit Waters Bull* 3:10–23
- Cardoso JFMF, Witte JIJ, van der Veer HW (2007a) Growth and reproduction of the bivalve *Spisula subtruncata* (da Costa) in Dutch coastal waters. *J Sea Res* 57:316–324 [doi:10.1016/j.seares.2006.12.002](https://doi.org/10.1016/j.seares.2006.12.002)
- Cardoso JFMF, Witte JIJ, van der Veer HW (2007b) Habitat related growth and reproductive investment in estuarine waters, illustrated for the tellinid bivalve *Macoma balthica* (L.) in the western Dutch Wadden Sea. *Mar Biol* 152:1271–1282 [doi:10.1007/s00227-007-0774-1](https://doi.org/10.1007/s00227-007-0774-1)
- Chu JW, Levin LA (1989) Photoperiod and temperature regulation of growth and reproduction in *Streblospio benedicti* (Polychaeta: Spionidae). *Invertebr Reprod Dev* 15:131–142 [doi:10.1080/07924259.1989.9672033](https://doi.org/10.1080/07924259.1989.9672033)
- Clancy N (1997) Environmental and population-specific contributions to growth rate variation in the marine amphipod *Jassa marmorata* Holmes. *J Exp Mar Biol Ecol* 209:185–200 [doi:10.1016/S0022-0981\(96\)02683-4](https://doi.org/10.1016/S0022-0981(96)02683-4)
- Conan G, Shafee MS (1978) Growth and biannual recruitment of the black scallop *Chlamys varia* (L.) in lanveoc area, Bay of Brest. *J Exp Mar Biol Ecol* 35:59–71 [doi:10.1016/0022-0981\(78\)90090-4](https://doi.org/10.1016/0022-0981(78)90090-4)
- Corey S (1969) The comparative life histories of three Cumacea (Crustacea): *Cumopsis goodsiri* (Van Beneden), *Iphinoe trispinosa* (Goodsir), and *Pseudocuma longicornis* (Bate). *Can J Zool* 47:695–704 [doi:10.1139/z69-116](https://doi.org/10.1139/z69-116)
- Dauvin JC (1988) Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 1. *Ampelisca tenuicornis* Liljeborg. *J Exp Mar Biol Ecol* 118:55–84 [doi:10.1016/0022-0981\(88\)90122-0](https://doi.org/10.1016/0022-0981(88)90122-0)
- Dauvin JC, Gentil F (1989) Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (Western English Channel). *Mar Biol* 103:63–73 [doi:10.1007/BF00391065](https://doi.org/10.1007/BF00391065)
- Dekker R, Beukema JJ (1993) Dynamics and growth of a bivalve, *Abra tenuis*, at the northern edge of its distribution. *J Mar Biol Assoc UK* 73:497–511 [doi:10.1017/S0025315400033063](https://doi.org/10.1017/S0025315400033063)
- Dekker R, Beukema JJ (1999) Relations of summer and winter temperatures with dynamics and growth of two bivalves, *Tellina tenuis* and *Abra tenuis*, on the northern edge of their intertidal distribution. *J Sea Res* 42:207–220 [doi:10.1016/S1385-1101\(99\)00026-X](https://doi.org/10.1016/S1385-1101(99)00026-X)
- Delgado L, Guerao G, Ribera C (1997) Biology of the mysid *Mesopodopsis slabberi* (van Beneden, 1861) (Crustacea, Mysidacea) in a coastal lagoon of the Ebro delta (NW Mediterranean). *Hydrobiologia* 357:27–35 [doi:10.1023/A:1003118332417](https://doi.org/10.1023/A:1003118332417)
- Desdevises Y, Maillet V, Fuentes M, Escriva H (2011) A snapshot of the population structure of *Branchiostoma lanceolatum* in the Racou Beach, France, during its spawning season. *PLoS One* 6:e18520 [PubMed doi:10.1371/journal.pone.0018520](https://pubmed.ncbi.nlm.nih.gov/doi/10.1371/journal.pone.0018520)
- Emig CC (1982) The biology of Phoronida. *Adv Mar Biol* 19:1–89 [doi:10.1016/S0065-2881\(08\)60086-3](https://doi.org/10.1016/S0065-2881(08)60086-3)

- Emson RH, Whitfield PJ (1989) Aspects of the life history of a tide pool population of *Amphipholis squamata* (Ophiuroidea) from South Devon. *J Mar Biol Assoc UK* 69:27–41 [doi:10.1017/S0025315400049080](https://doi.org/10.1017/S0025315400049080)
- Enders HE (1909) A study of the life-history and habits of *Chaetopterus variopedatus* Renier et Claparede. *J Morphol* 20:479–531 [doi:10.1002/jmor.1050200306](https://doi.org/10.1002/jmor.1050200306)
- Fish S (1970) The biology of *Eurydice Pulchra* [Crustacea: Isopoda]. *J Mar Biol Assoc UK* 50:753–768 [doi:10.1017/S0025315400005026](https://doi.org/10.1017/S0025315400005026)
- Franke HD, Beermann J (2014) The influence of intrinsic and extrinsic factors on developmental parameters and their relationships in the marine isopod *Idotea linearis* (Crustacea). *Hydrobiologia* 732:197–212 [doi:10.1007/s10750-014-1846-0](https://doi.org/10.1007/s10750-014-1846-0)
- Freeman SM, Richardson CA, Seed R (2001) Seasonal abundance, spatial distribution, spawning and growth of *Astropecten irregularis* (Echinodermata: Asteroidea). *Estuar Coast Shelf Sci* 53:39–49 [doi:10.1006/ecss.2000.0758](https://doi.org/10.1006/ecss.2000.0758)
- Gage JD (1990) Skeletal growth bands in brittle stars: microstructure and significance as age markers. *J Mar Biol Assoc UK* 70:209–224 [doi:10.1017/S0025315400034329](https://doi.org/10.1017/S0025315400034329)
- Gaspar MB, Castro M, Monteiro CC (1995) Age and growth rate of the clam, *Spisula solida* L., from a site off Vilamoura, south Portugal, determined from acetate replicas of shell sections. *Sci Mar* 59:87–93
- George CL, Warwick RM (1985) Annual macrofauna production in a hard-bottom reef community. *J Mar Biol Assoc UK* 65:713–735 [doi:10.1017/S0025315400052553](https://doi.org/10.1017/S0025315400052553)
- Giangrande A, Frascetti S (1993) Life cycle, growth and secondary production in a brackish-water population of the polychaete *Notomastus latericeus* (Capitellidae) in the Mediterranean Sea. *PSZNI: Mar Ecol* 14:313–327 [doi:10.1111/j.1439-0485.1993.tb00003.x](https://doi.org/10.1111/j.1439-0485.1993.tb00003.x)
- Gudmundsson H (1985) Life history patterns of polychaete species of the family Spionidae. *J Mar Biol Assoc UK* 65:93–111 [doi:10.1017/S0025315400060835](https://doi.org/10.1017/S0025315400060835)
- Guillou J, Sauriau PG (1985) Some observations on the biology and ecology of a *Venus striatula* population in the bay of Douardenez, Brittany. *J Mar Biol Assoc UK* 65:889–900 [doi:10.1017/S0025315400019391](https://doi.org/10.1017/S0025315400019391)
- Heffernan P (1985) Demography of *Pholoe minuta* (Polychaeta: Sigalionidae) in Galway Bay, west coast of Ireland, with special reference to settlement and recruitment patterns. *Mar Biol* 84:323–329 [doi:10.1007/BF00392502](https://doi.org/10.1007/BF00392502)
- Henderson PA, Holmes RHA (1987) On the population biology of the common shrimp *Crangon crangon* (L.) (Crustacea: Caridea) in the Severn Estuary and Bristol Channel. *J Mar Biol Assoc UK* 67:825–847 [doi:10.1017/S0025315400057076](https://doi.org/10.1017/S0025315400057076)
- Henderson SM, Richardson CA (1994) A comparison of the age, growth rate and burrowing behaviour of the razor clams, *Ensis siliqua* and *E. ensis*. *J Mar Biol Assoc UK* 74:939–954 [doi:10.1017/S0025315400090160](https://doi.org/10.1017/S0025315400090160)
- Jensen M (1969) Breeding and growth of *Psammechinus miliaris* (Gmelin). *Ophelia* 7:65–78 [doi:10.1080/00785326.1969.10419289](https://doi.org/10.1080/00785326.1969.10419289)
- Jensen JN (1990) Increased abundance and growth of the suspension-feeding bivalve *Corbula gibba* in a shallow part of the eutrophic Limfjord, Denmark. *Neth J Sea Res* 27:101–108 [doi:10.1016/0077-7579\(90\)90038-I](https://doi.org/10.1016/0077-7579(90)90038-I)
- Kanneworff E (1965) Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* Liljeborg from the Øresund. *Ophelia* 2:305–318 [doi:10.1080/00785326.1965.10409606](https://doi.org/10.1080/00785326.1965.10409606)
- Kideys AE (1996) Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgol Meeresunters* 50:353–368 [doi:10.1007/BF02367109](https://doi.org/10.1007/BF02367109)
- Kirkegaard B (1970) Age determination of *Nephtys* (Polychaeta: nephtyidae). *Ophelia* 7:277–281 [doi:10.1080/00785236.1970.10419301](https://doi.org/10.1080/00785236.1970.10419301)
- Krevrekidis T (2005) Population dynamics, reproductive biology and productivity of *Streblospio shrubsolii* (Polychaeta: Spionidae) in different sediments at low salinities in a Mediterranean lagoon (Monolimni Lagoon, Northern Aegean). *Int Rev Hydrobiol* 90:100–121 [doi:10.1002/iroh.200310713](https://doi.org/10.1002/iroh.200310713)

- Kristensen E (1984) Life cycle, growth and production in estuarine populations of the polychaetes *Nereis virens* and *N. diversicolor*. *Ecography* 7:249–250 [doi:10.1111/j.1600-0587.1984.tb01128.x](https://doi.org/10.1111/j.1600-0587.1984.tb01128.x)
- López-Jamar E, González G, Mejuto J (1987) Ecology, growth and production of *Thyasira flexuosa* (Bivalvia, Lucinacea) from Ría de la Coruña, North-West Spain. *Ophelia* 27:111–126 [doi:10.1080/00785236.1987.10422015](https://doi.org/10.1080/00785236.1987.10422015)
- Manjón-Cabeza ME, Garcia-Raso JE (1998) Population structure and growth of the hermit crab *Diogenes pugilator* (Decapoda: Anomura: Diogenidae) from the Northeastern Atlantic. *J Crustac Biol* 18:753–762 [doi:10.2307/1549152](https://doi.org/10.2307/1549152)
- Mcclusky DS (1967) Some Effects of salinity on the survival, moulting, and growth of *Corophium volutator* [Amphipoda]. *J Mar Biol Assoc UK* 47:607–617 [doi:10.1017/S0025315400035220](https://doi.org/10.1017/S0025315400035220)
- Neuparth T, Costa FO, Costa MH (2002) Effects of temperature and salinity on life history of the marine amphipod *Gammarus locusta*. Implications for ecotoxicological testing. *Ecotoxicology* 11:61–73 [PubMed doi:10.1023/A:1013797130740](https://pubmed.ncbi.nlm.nih.gov/1013797130740/)
- Nichols D, Barker MF (1984) Growth of juvenile *Asterias rubens* L. (Echinodermata: Asteroidea) on an intertidal reef in southwestern Britain. *J Exp Mar Biol Ecol* 78:157–165 [doi:10.1016/0022-0981\(84\)90076-5](https://doi.org/10.1016/0022-0981(84)90076-5)
- Ockelmann KW, Muus K (1978) The biology, ecology and behaviour of the Bivalve *Mysella bidentata* (Montagu). *Ophelia* 17:1–93 [doi:10.1080/00785236.1978.10425474](https://doi.org/10.1080/00785236.1978.10425474)
- Ockelmann KW, Vahl O (1970) On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia* 8:275–294 [doi:10.1080/00785236.1970.10429564](https://doi.org/10.1080/00785236.1970.10429564)
- Peharda M, Ezgeta-Balić D, Radman M, Sinjkević N, Vrgoč N, Isajlović I (2012) Age, growth and population structure of *Acanthocardia tuberculata* (Bivalvia: Cardiidae) in the eastern Adriatic Sea. *Sci Mar* 76:59–66 [doi:10.3989/scimar.03257.21A](https://doi.org/10.3989/scimar.03257.21A)
- Pluscheva M, Martin D, Britayev T (2004) Population ecology of two sympatric polychaetes, *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae), in the White Sea. *Invertebrate Zoology* 1:65–73 [doi:10.15298/invertzool.01.1.06](https://doi.org/10.15298/invertzool.01.1.06)
- Price R, Warwick RM (1980) Temporal variations in annual production and biomass in estuarine populations of the two polychaetes, *Nephtys hombergii* and *Ampharete acutifrons*. *J Mar Biol Assoc UK* 60:481–487 [doi:10.1017/S0025315400028496](https://doi.org/10.1017/S0025315400028496)
- Ridgway ID, Richardson CA (2011) *Arctica islandica*: the longest lived non-colonial animal known to science. *Rev Fish Biol Fish* 21:297–310 [doi:10.1007/s11160-010-9171-9](https://doi.org/10.1007/s11160-010-9171-9)
- Rowden AA, Jones MB (1994) A contribution to the biology of the burrowing mud shrimp, *Callinassa subterranea* (Decapoda: Thalassinidea). *J Mar Biol Assoc UK* 74:623–635 [doi:10.1017/S0025315400047706](https://doi.org/10.1017/S0025315400047706)
- Sejr MK, Sand MK, Jensen KT, Petersen JK, Christensen PB, Rysgaard S (2002) Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). *Mar Ecol Prog Ser* 244:163–169 [doi:10.3354/meps244163](https://doi.org/10.3354/meps244163)
- Selin NI (2007) Shell form, growth and life span of *Astarte arctica* and *A. borealis* (Mollusca: Bivalvia) from the subtidal zone of northeastern Sakhalin. *Russ J Mar Biol* 33:232–237 [doi:10.1134/S1063074007040050](https://doi.org/10.1134/S1063074007040050)
- Sköld M, Loo LO, Rosenberg R (1994) Production, dynamics and demography of an *Amphiura filiformis* population. *Mar Ecol Prog Ser* 103:81–90 [doi:10.3354/meps103081](https://doi.org/10.3354/meps103081)
- Sola JC (1996) Population dynamics, reproduction, growth, and secondary production of the mud-snail hydrobia ulvae (Pennant). *J Exp Mar Biol Ecol* 205:49–62 [doi:10.1016/S0022-0981\(96\)02597-X](https://doi.org/10.1016/S0022-0981(96)02597-X)
- Swennen C, Leopold MF, Stock M (1985) Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. *Helgol Meeresunters* 39:255–261 [doi:10.1007/BF01992773](https://doi.org/10.1007/BF01992773)
- Thiel M (1998) Population biology of *Dyopededos monacanthus* (Crustacea: Amphipoda) on estuarine soft-bottoms: importance of extended parental care and pelagic movements. *Mar Biol* 132:209–221 [doi:10.1007/s002270050387](https://doi.org/10.1007/s002270050387)

- Tuck ID, Chapman CJ, Atkinson RJA (1997) Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. I. Growth and density. *ICES J Mar Sci* 54:125–135 [doi:10.1006_jmsc.1996.0179](https://doi.org/10.1006/jmsc.1996.0179)
- Tunberg B (1983) Growth of *Dosinia exoleta* (L.) (Bivalvia) in Raunefjorden, western Norway. *Sarsia* 68:40–45 [doi:10.1080_00364827.1983.10420556](https://doi.org/10.1080_00364827.1983.10420556)
- Tunberg B (1983) Population Structure, Size Distribution, and Shell Growth of *Dosinia Lupinus* (L.) (Bivalvia) in Raunefjorden, Western Norway, with Biometrical Comparison to *Dosinia Exoleta* (L.). *Sarsia* 68:33–40 [doi:10.1080_00364827.1983.10420555](https://doi.org/10.1080_00364827.1983.10420555)
- Valentin C, Anger K (1977) In-situ Studies on the Life Cycle of *Diastylis rathkei* (Cumacea: Crustacea). *Mar Biol* 39:71–76 [doi:10.1007_BF00395596](https://doi.org/10.1007_BF00395596)
- Van Hoey G 2006. Spatio-temporal variability within the macrobenthic *Abra alba* community, with emphasis on the structuring role of *Lanice conchilega*. PhD Thesis, Ghent University, Belgium, 187 pp.
- Warren LM (1976) A population study of the polychaete *Capitella capitata* at Plymouth. *Mar Biol* 38:209–216 [doi:10.1007_BF00388934](https://doi.org/10.1007_BF00388934)
- Warwick RM, George CL, Davies JR (1978) Annual macrofauna production in a Venus community. *Estuar Coast Mar Sci* 7:215–241 [doi:10.1016_0302-3524\(78\)90107-X](https://doi.org/10.1016_0302-3524(78)90107-X)
- Yamada SB, Dumbauld BR, Kalin A, Hunt CE, Figlar-Barnes R, Randall A (2005) Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. *Biol Invasions* 7:309–321 [doi:10.1007_s10530-004-0877-2](https://doi.org/10.1007_s10530-004-0877-2)
- Yonow N, Ryland JS 1992. Growth and life history parameters in *Acteon tornatilis* (L.) (Opisthobranchia: Cephalaspidea). *Marine Eutrophication and Population Dynamics*. Proc. 25th EMBS (eds G Colombo et al.), pp 271 – 276

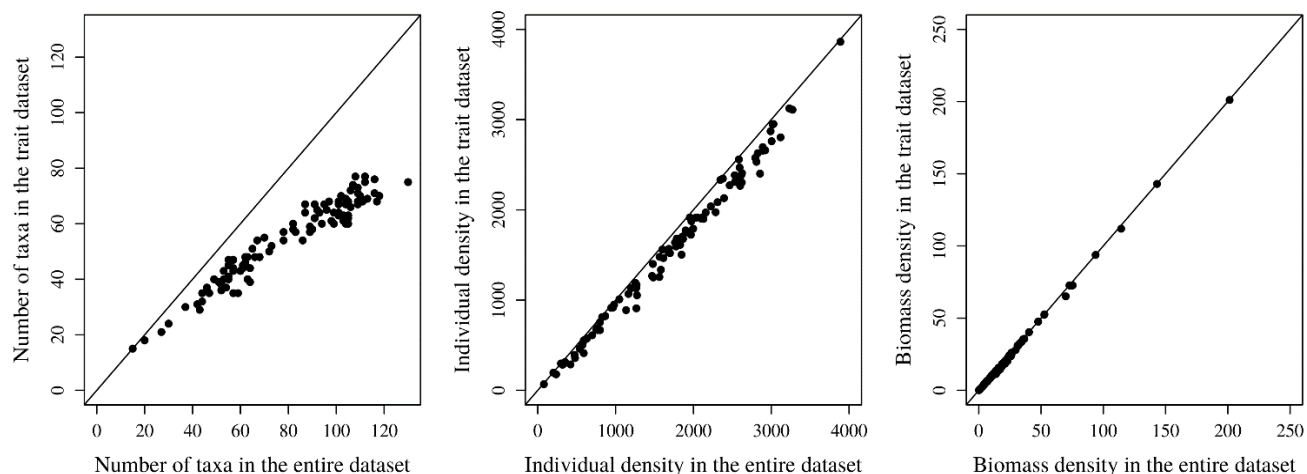


Figure S1. Comparison between the whole taxocenosis (391 taxa) and its subset documented for biological traits (190 taxa). The three basic community descriptors, number of taxa, individual density (number of individual organisms m^{-2}) and biomass density (ash-free dry weight $g m^{-2}$), were calculated for each of the 103 sampling stations (black dots, values averaged over the period 1995 – 2015).

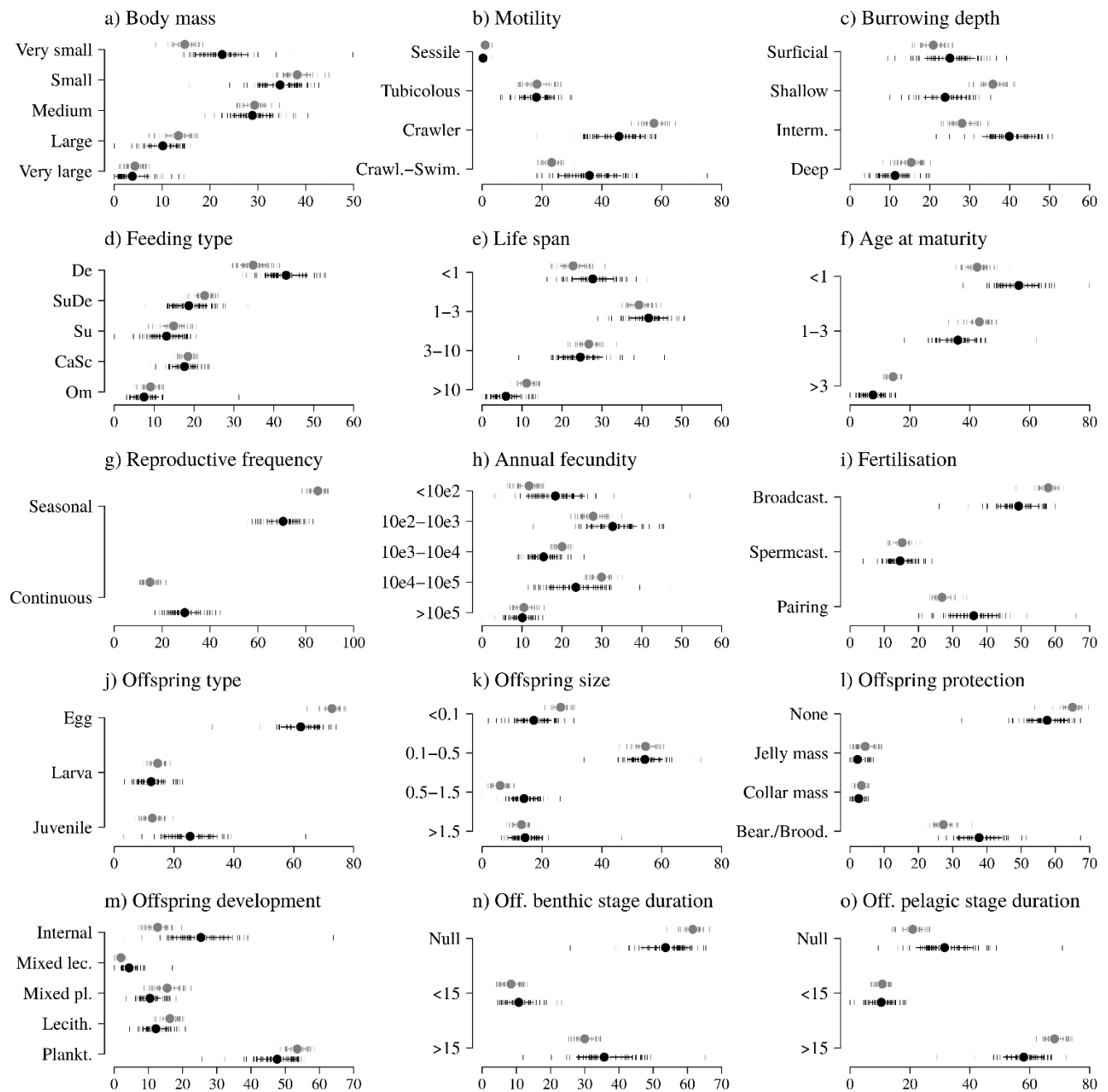


Figure S2. Trait modality distributions over the whole area. Trait modalities are represented as percentages of species within communities. Dot, mean \pm SD. Grey, low dynamics; black, high dynamics. Within a community (vertical segment), modality scores sum to 100% within the considered trait. Feeding type: Su, suspension feeder; De, deposit feeder; CaSc, carnivore-scavenger; Om, omnivore. Globally, the high dynamics habitat is more functionally heterogeneous (mean SD = 5.26) than the low dynamics one (mean SD = 2.52)

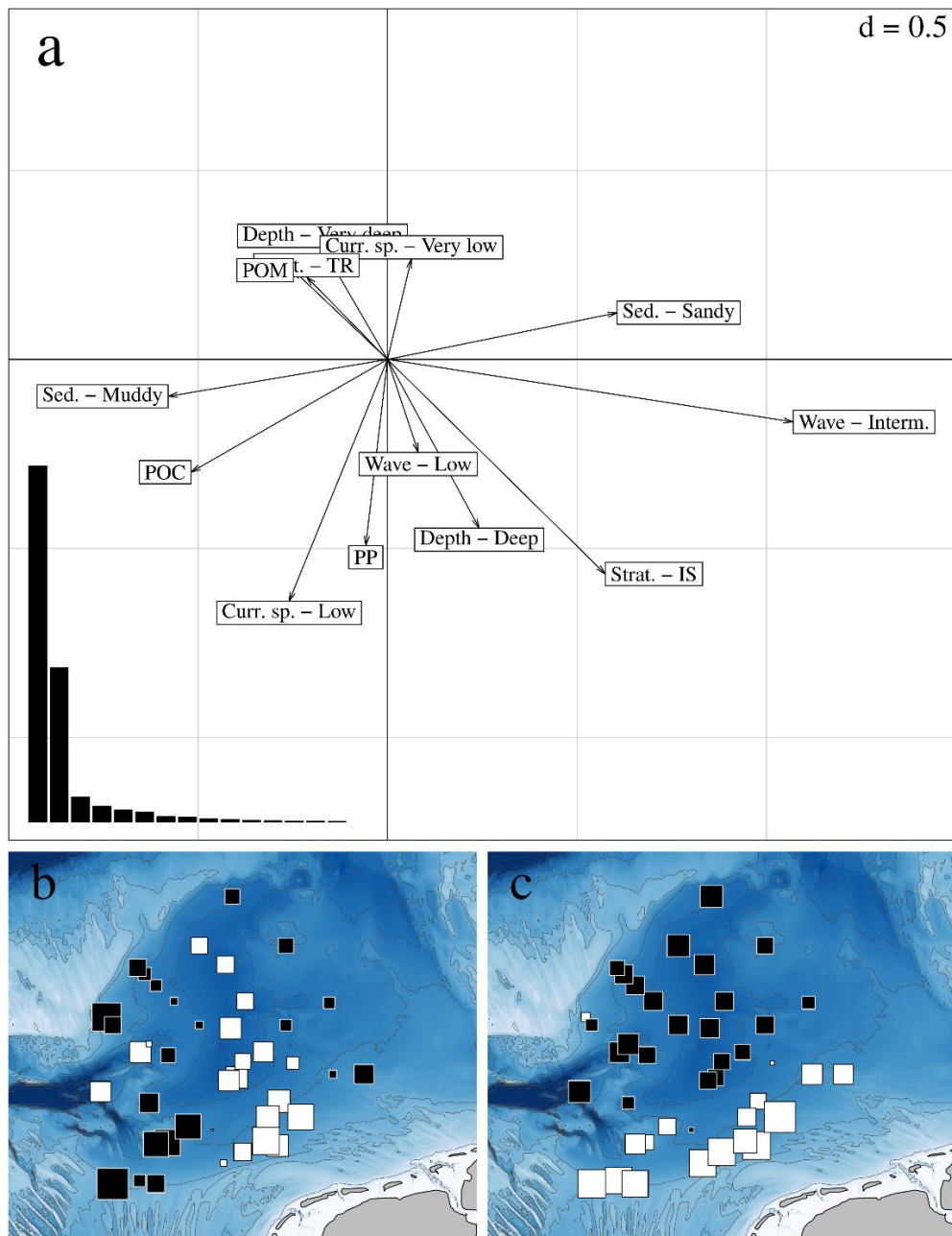


Figure S3. RLQ analysis of the low dynamics habitat. a) Habitat descriptors projected onto axes 1 and 2; “d” indicates the grid scale; bar diagram, eigenvalues (axis 1, 60%; axis 2, 26%); for clarity, only the significant modalities of qualitative variables are shown (according to Table S4). Abbreviations: Curr. sp., current speed; Intern., intermediate; POC, particulate organic carbon; PP, primary productivity; Sed., sediment; Strat., stratification (IS, intermittently stratified; TR, transitional). b) Station axis score 1. c) Station axis score 2. White squares, low scores; black squares, high scores; square size, proportional to the deviation from the mean



Figure S4. RLQ analysis of the low dynamics habitat. Distributions of trait modalities (ellipses) respective to each trait (windows); blue dots, species positions; trait modalities are positioned at the gravity center of their respective species. Only traits significantly related to the axes are represented. “d” indicates the grid scale

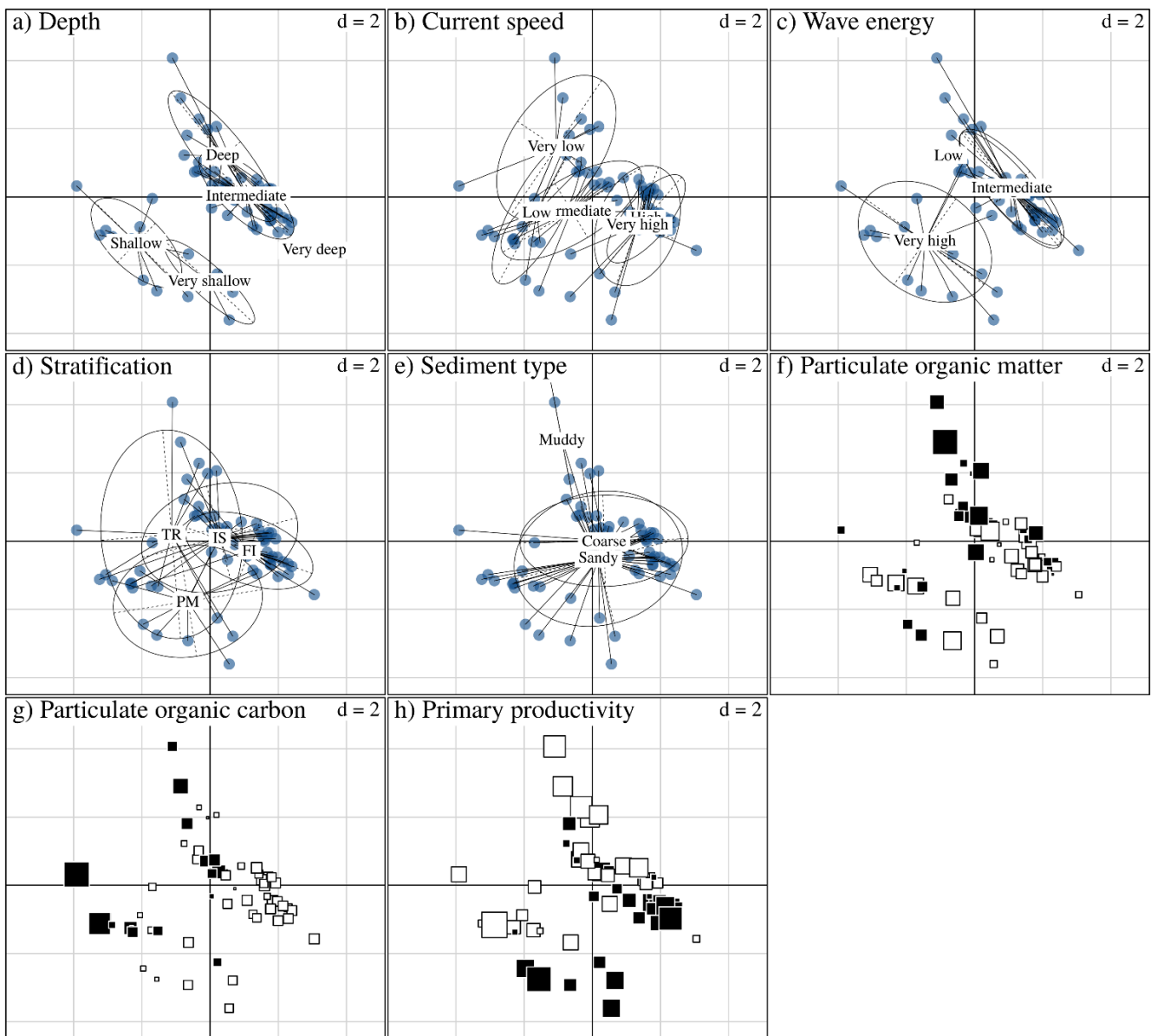


Figure S5. Detailed distributions of habitat descriptors in the high dynamics analysis (complementary to Fig. 4). Blue dots (a-e) and squares (f-h) indicate positions of sampling stations. d) IS, intermittently stratified; FI, freshwater influence; PM, permanently mixed; TR, transitional. f-h) White squares, low values; black squares, high values; square sizes are proportional to the deviation from the mean value. “d” indicates the grid scale

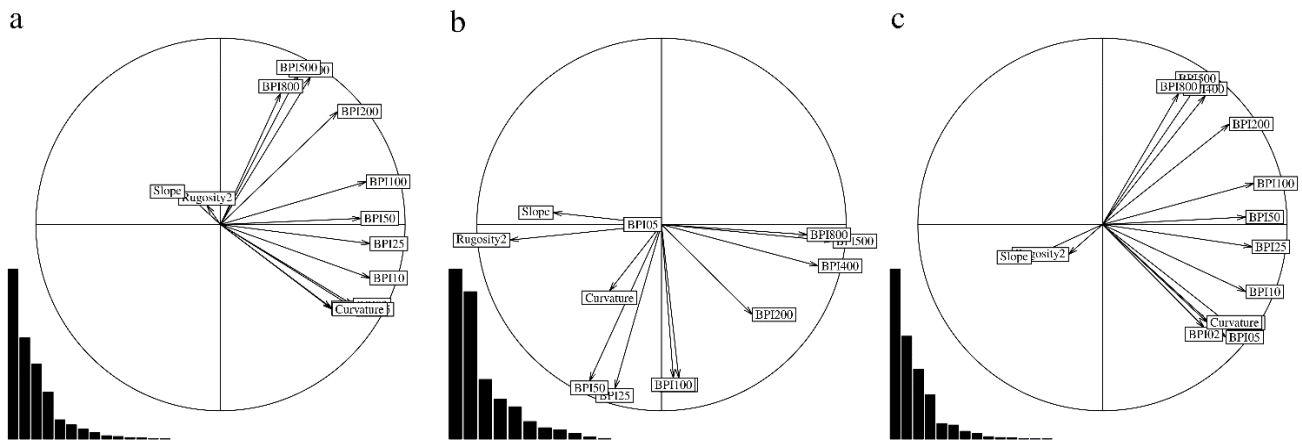


Figure S6. PCAs on geomorphological data, correlation circles of axis 1 and 2. a) Large scale. b) Low dynamics. c) High dynamics. Bar diagrams, eigenvalues. A common feature to the three patterns consists in positive correlations between large scale BPIs along the first axis (from left to right). Except in low dynamics, the second axis expresses a synthetic opposition between large scale (upward) and small scale (downward) BPIs. Third and fourth axes in a and c, although suggestive, are stretched only by a few stations with extreme scores

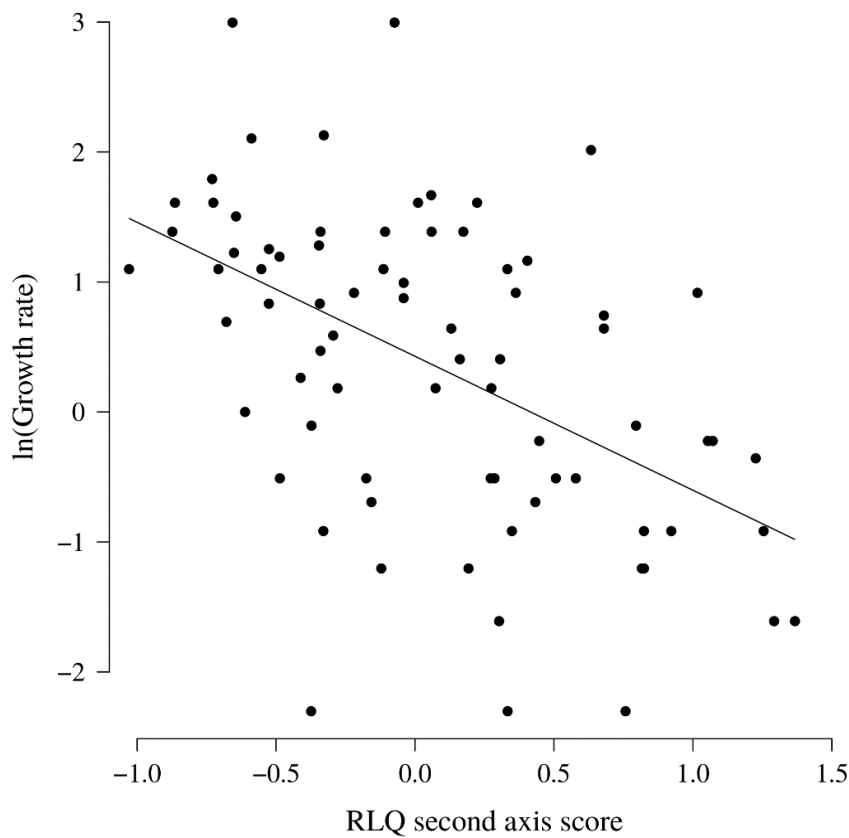


Figure S7. Relationship between taxon growth rate and the second RLQ axis of the high dynamics habitat analysis. Growth rate, prior to be \ln -transformed, was measured in cm year^{-1} . $n = 77$, $r = 0.51$, $p < 0.001$. Growth rate data provided in Table S6