

A generic approach to develop a trait-based indicator of trawling-induced disturbance

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ABSTRACT: Biological trait analysis has become a popular tool to infer the vulnerability of benthic species to trawling-induced disturbance. Approaches using multiple traits are being developed, but their generic relevance across faunal components and geographic locations remains poorly tested, and the importance of confounding effects are poorly recognised. This study integrates biological traits of benthic species that are responsive to instantaneous effects of trawling (i.e. sensitivity) and traits expressing recoverability over the longer term (i.e. years). We highlight the functional independence between these 2 components in response to trawling, test the behaviours of single and combined traits and account for potential confounding effects of environment and trawling intensity on benthic communities through variation partitioning. Two case studies are considered: epibenthos from the Bay of Biscay and endobenthos of the Dutch sector of the North Sea. The response to trawling is most pronounced when multiple traits covering different aspects that determine population dynamics (i.e. sensitivity and recoverability) are combined, despite confounding effects between gradients of benthic production and trawling intensity, especially for endobenthos. The integration of traits reflecting both sensitivity and recoverability provides complementary information on the faunal response to trawling, bridging the gap between fishing impact assessments and benthic community status assessments.

KEY WORDS: Benthic macroinvertebrate · Bottom trawling · Natural history · Biological trait · Composite indicator · Time scale · Confounding effect

1. INTRODUCTION

The state of seabed habitats, and how benthic communities are affected by the physical disturbance caused by mobile bottom-fishing gears, can be assessed using well-established quantitative methods (Hiddink et al. 2017, Pitcher et al. 2017, Sciberras et al. 2018, Rijnsdorp et al. 2020). These are based on a simple equation for relative benthic status that includes parameters for the instantaneous effect caused by the passing of the gear, termed depletion, and recovery over the longer term. Ecosystem-based fisheries management now also requires an assessment of the state of seabed habitats in terms of their typical species composition, the abundance of particularly sensitive or fragile species or their functioning. At present, there is no consensus on how these different aspects of the benthic community are affected by fishing-induced physical disturbance in terms of both the depletion and the recovery processes, thereby hampering support to management decisions.

Assessing the status of benthic communities does not generally take into account differences in life history characteristics that may affect organism responses to, and capacity of populations to recover from, changing environments (Tyler-Walters et al. 2009). Depletion and recovery rates following physical disturbance tend to be estimated for whole benthic communities in generic habitats (Kaiser et

al. 2006, Sciberras et al. 2018) which may not be representative of specific aspects of the benthic community occurring in a local habitat. Consequently, the use of trait information to infer the vulnerability of species to disturbance by proxy is increasingly being explored as a complementary approach (Beauchard et al. 2017).

Tyler-Walters et al. (2009) introduced the concepts of species' 'intolerance' and 'recoverability' to trawling disturbance, subsequently developed further by Bolam et al. (2014) as 'instantaneous sensitivity' and 'long-term sensitivity'. Here, we expand such approaches, using the term 'sensitivity' to indicate the extent to which a species is likely to be affected by the passage of a trawl, and 'recoverability' to indicate the capacity of a population to recover from the disturbance and the timescale over which recovery will occur. Recent studies have considered the use of multiple traits for assessing the sensitivity of marine benthos to bottom trawling using composite indicators based on scored trait modalities (de Juan & Demestre 2012, Bolam et al. 2014, Foveau et al. 2017, González-Irusta et al. 2018, Mérillet et al. 2018, Hinz et al. 2021). The general relevance of using functional traits in such a framework was confirmed in a study on the vulnerability of demersal fish assemblages to trawling, where the combination of catchability and resistance represented sensitivity while resilience represented recoverability (de Juan et al. 2020).

Scientific consensus exists on the mechanisms underlying the response of benthic communities to physical disturbance (hereafter 'trawling') on the sea floor (International Council for the Exploration of the Sea 2017a, Pitcher et al. 2017, Rijnsdorp et al. 2018). Organism densities can decline following the passage of a trawl, as a result of death or removal of the affected fauna (i.e. depletion). Recovery may take place after this initial effect, potentially until the community returns to its untrawled state. The latter depends on the intrinsic rate of natural increase of the species. Whether full recovery occurs or, if not, what alternative equilibrium the community may reach, depends on the magnitude and frequency of trawling, as well as the recovery potential of the community. If trawling is sufficiently frequent, communities may not have time to recover entirely between trawling events, leading to longer-term shifts in community composition with increased dominance of less sensitive species and lower densities or extirpation of the more vulnerable species.

There is a simple trade-off between recoverability and vulnerability. Species with high intrinsic rate of natural increase are generally considered to have higher potential to recover to pre-disturbance densities, and consequently to be less vulnerable. The intrinsic rate of natural increase results from a combination of growth and reproductive traits that favour population expansion. However, other traits that are not directly related to population growth are also relevant to sensitivity and recovery. The importance of these traits may manifest at different spatio-temporal scales. For example, a trait related to sensitivity such as an armoured body may provide some defence from the immediate physical effects of a trawl, but only if the trawl makes contact with an individual directly. In addition to processes within the footprint of the trawl, such as growth of surviving fauna, recovery may also be influenced by traits reflecting larger-scale factors such as the ability of an organism to recruit and recolonise, or to actively migrate into the trawled area. These processes may be determined by the densities of adult organisms in adjacent (in case of mobility) or more distant (through larval transport) areas. It follows that species with low recovery potential may not be sensitive to disturbance, for example slow-growing species which are deep burrowers (Bergman & van Santbrink 2000). Conversely, species with high recoverability may be sensitive if disturbance exceeds a frequency at which they are depleted, for example fragile epibenthic organisms such as Bryozoa including *Flustra foliacea* (Bitschofsky et al. 2011).

Usually, studies either focus on a single trait (i.e. longevity, Rijnsdorp et al. 2020) or combine several traits to explain the response of the benthic community to trawling. Such approaches, however, only cover part of the recovery aspect in case of a single trait and ignore entirely the depletion aspect in all cases. As part of a more comprehensive and generic approach, we used biological traits representing the instantaneous effect of the passage of a trawl, i.e. sensitivity, and traits representing the longer-term recoverability. We applied these to endobenthos from the Dutch sector of the North Sea and epibenthos from the Bay of Biscay. We hypothesized as follows: (1) traits reflecting the sensitivity and recovery of a benthic community to trawling are independent and provide complementary information on the community's vulnerability; (2) combined traits are more responsive to trawling than individual traits.

To test H1, we defined a series of benthic community traits related to sensitivity and recoverability, and analysed the relationships between these traits to explore the degree of independence between the 2

components. Based on the 2 case studies, we tested H2 by analysing relationships between field organism density data weighted by those traits, and data on trawling intensity; these relationships were expected to be negative. Importantly, while doing this, we corrected for the potentially confounding effects of environmental variation on these relationships. Although this work is intended to provide information to support the development of a generic indicator accounting for the interdependence of sensitivity and recovery, we propose a specific version adapted to areas with long histories of fishing exploitation.

2. MATERIALS AND METHODS

2.1. Biological traits

Different biological traits from larval, juvenile and adult stages determine population vulnerability to trawling. Some traits are relevant to the instantaneous effect of the passage of a trawl ('sensitivity'), while entirely different traits may represent the capacity of organisms and their populations to recover from trawling ('recoverability').

2.1.1. Sensitivity

Some species are fragile and easily damaged, while others are more robust. A buried organism is less likely to be exposed to trawling than an epibenthic one, with a greater chance of survival as its burrowing depth increases. Direct exposure to trawling can be mitigated by body size. Smaller species are generally less sensitive than larger-bodied taxa, as the former can escape through a net more easily if captured (Bolam et al. 2014, González-Irusta et al. 2018). The sensitivity (SE) component of a benthic assemblage can therefore be expected to be a function of standardised body fragility, burrowing depth and body length. In previous and similar works, composite indicators were built by adding trait scores. In this context, multiplicative aggregation is preferable due to (possibly irrelevant) compensatory effects of additive aggregation (Gan et al. 2017). For instance, a small body length (low sensitivity) buffers the high sensitivity of epibenthic living mode: the low sensitivity score of the former penalizes the high sensitivity score of the latter, more by multiplication than addition (e.g. $1 \times 3 < 1 + 3$); such scores are presented in more detail in Section 2.2 (see also Table 1). With this in mind, SE is defined here as:

$$SE = FR \times BD \times BL \quad (1)$$

where FR is fragility, BD is burrowing depth, and BL is body length.

2.1.2. Recoverability

Mobile species are likely to recolonise a trawled area by migrating more quickly than less mobile species, so recoverability is likely to be a function of motility (MO). Recoverability also depends on recruitment from larval settlement and subsequent growth to the adult stage. Late-maturing, slow-growing or poorly-recruiting species will all have low recoverability (MacDonald et al. 1996). Life span (LS), as used in the 'longevity approach' of Rijnsdorp et al. (2018), and age at maturity (AM) are traits of critical importance. Some species require a long time to achieve minimal reproductive success, including those with the naturally high juvenile mortality that is often driven by stochastic environmental conditions (Kindsvater et al. 2016).

LS is expected to respond negatively to trawling intensity in habitats dominated by species that live for years or even decades (Rijnsdorp et al. 2020), as are often encountered in rarely disturbed benthic habitats (e.g. coral reefs). However, in areas where the seafloor has been intensively trawled for more than a century, such as the European continental shelves, the individual and biomass densities of long-lived organisms may be too low to detect significant trawling effects. In such areas, and especially under high trawling frequencies, AM expresses a more relevant critical aspect of the life cycle, namely the chance of experiencing at least one reproduction before being killed by a trawl, especially if reproductive life span (RLS = LS - AM), for the same AM, is reduced compared to truly long-lived species. In

general, AM is correlated with LS (Charnov 1993), and AM may account for a potential LS-effect. However, this relationship is not perfect when considering several phyla or limited spatial biogeographic extent. The AM/RLS ratio emphasises the critical time necessary to reach maturity and achieve reproductive success over a shorter RLS. For the same AM, very long-lived species, assumed to be largely depleted in intensively trawled areas, perform less successfully. However, the simple AM/RLS ratio can take the same value for species with different AM and RLS, so a species maturing at 1 yr of age and dying after 2 yr is assigned the same value as another species maturing at 2 yr and dying after 4 yr. To counteract this, the ratio can be multiplied by AM to introduce an appropriate penalty for RLS in long-lived species with late AM. We call the resultant term relative maturity (RM), with 1 added to RLS to deal with cases where LS = AM (semelparity, in which case RLS = 0), both measured in years:

$$RM = \frac{AM}{RLS + 1} \times AM \quad (2)$$

These age-related aspects are of paramount importance in life history strategies of organisms (Charnov 1993), but some independent traits relevant to reproduction and offspring may be complementary. In the marine benthos, offspring can be released by parents at different developmental stages, depending on the species, with different chances of survival before settling as juveniles. Broadcasted eggs in the water column are more vulnerable to planktotrophy than brooded larvae, and both are more vulnerable than juveniles released as ‘miniature adults’ after internal incubation (Giangrande et al. 1994, Pechenik 1999). Large eggs have a shorter critical pelagic phase, because of faster development, than smaller ones (Giangrande et al. 1994, Giangrande 1997). The potential for recovery (RE) of the benthic community will therefore be a function of motility (MO), offspring type (OT) and offspring size (OS) as well as RM. Generally, OS is negatively correlated with fecundity due to the constraints of energetic allocation (Kindsvater et al. 2016), whereas OT can be independent of fecundity (e.g. many bivalves broadcast millions of eggs, and some crabs brood millions of larvae). Hence, RE includes many relevant aspects of species’ life histories, and is defined here as:

$$RE = RM \times MO \times OT \times OS \quad (3)$$

2.1.3. Vulnerability

Finally, we defined vulnerability by combining SE and RE by addition and multiplication (SE + RE and SE × RE, respectively). Although we preferred multiplicative aggregation within the SE and RE components, we expected some independence between SE and RE, so that the 2 components could additively compensate each other without synergy (Gan et al. 2017). Hence, both additive and multiplicative variants of the combined components were calculated to compare their distributions and associated variations.

We tested H1 on the fauna from 2 case studies for which we compiled the described traits from the literature (next sections). Then, prior to testing H2, we compared SE and RE distributions to assess their degree of variation, especially between the additive and multiplicative variants of vulnerability. As part of testing H2, for each case study, the taxa × traits matrix (including individual traits, trait combinations, SE, RE and vulnerability) was combined with survey data to examine relationships between trait-weighted organism densities and trawling intensity.

2.2. Trait data

Trait data were sought for all taxa found in the 2 case studies (see Table S1), mostly at the species and genus level. Trait information was obtained from peer-reviewed articles (n = 466), with additional books and book chapters (27), academic theses (25) and documents from the grey literature (14). Online data bases (7) were used when source information was not accessible. Trait information for the Bay of Biscay was complemented using the MERP Trait Explorer (Marine Ecosystem Research Programme 2021). In some cases, in absence of information at the species level, information of species from the same genus was used. For the Dutch exclusive economic zone (EEZ), we were able to obtain functional

trait information for species that accounted for 94 and 85% of individual and biomass densities, respectively. For the Bay of Biscay, these percentages reached 87 and 95% respectively, after removing highly mobile species (fish and large cephalopods). Traits of 330 taxa in total were documented, 195 from the Dutch EEZ and 148 from the Bay of Biscay. Only 13 taxa were common to both case studies. Functionally, there were 217 unique trait combinations, 146 for the Dutch EEZ and 92 for the Bay of Biscay, with 21 trait combinations in common.

Most traits had ordinal modalities. These were ranked according to their responsiveness to trawling in such a way that all responses to trawling were expected to be negative. No a priori weights could be attributed to the traits, so they were considered to be of equal importance and simply standardised to range between 0 and 1. Traits, their modalities and scores are shown in Table 1.

Table 1. Traits and their modalities. Scores express the relative degree of responsiveness of each trait to physical disturbance

| Trait | Modality | Raw score | Standardized score | |
|----------------------------------|----------------------|-----------------|--------------------|------|
| Fragility | Robust | 1 | 0.00 | |
| | Intermediate | 2 | 0.50 | |
| | Fragile | 3 | 1.00 | |
| Sensitivity | Burrowing depth (cm) | >15 | 1 | 0.00 |
| | | 5-15 | 2 | 0.33 |
| | | 0-5 | 3 | 0.67 |
| | | 0 | 4 | 1.00 |
| Sensitivity | Body length (cm) | <1 | 1 | 0.00 |
| | | 1-3 | 2 | 0.25 |
| | | 3-10 | 3 | 0.50 |
| | | 10-20 | 4 | 0.75 |
| | | >20 | 5 | 1.00 |
| Age at maturity (years) | <1 | 1 | 0.00 | |
| | 1-3 | 2 | 0.50 | |
| | >3 | 3 | 1.00 | |
| Life span (years) | <1 | 1 | 0.00 | |
| | 1-3 | 2 | 0.33 | |
| | 3-10 | 3 | 0.67 | |
| | >10 | 4 | 1.00 | |
| Recoverability | Motility | Crawler-Swimmer | 1 | 0.00 |
| | | Crawler | 2 | 0.33 |
| | | Tubicolous | 3 | 0.67 |
| | | Sessile | 4 | 1.00 |
| Offspring type | Juvenile | 1 | 0.00 | |
| | Larva | 2 | 0.50 | |
| | Egg | 3 | 1.00 | |
| Offspring size (μm) | >1500 | 1 | 0.00 | |
| | 500-1500 | 2 | 0.33 | |
| | 100-500 | 3 | 0.67 | |
| | <100 | 4 | 1.00 | |

2.3. Benthic survey data

The responsiveness to trawling intensity of individual traits, and SE and RE components separately and in different (additive and multiplicative) combinations, were tested using benthic data from 2 case studies: endobenthos from the Dutch EEZ and mega-epibenthos from the Bay of Biscay, sampled using box corer and trawl, respectively (Fig. 1). The trawl proportionally samples larger organisms and more efficiently epibenthic and dispersed species. Hence, differences in functional attributes of the 2 faunas were expected given the contrasting sampling techniques.

2.3.1. Dutch EEZ

The study area ranges from 51.62 to 55.47° N. Its bottom, from shallow to deeper areas (50 m), is mostly sandy with local mud patches, especially in the deep northern part (Oyster Ground), characterised by much lower tidal velocities than in the south. Stations (n = 79) (Fig. 1a), excluding coastal stations heavily impacted by shrimp trawling, were sampled annually from 1995 to 2010, and then in 2012 and 2015. Sediment was sampled with a box corer (1 core per station, 0.08 m², 15 cm deep), and macrozoobenthos was separated using a 1 mm mesh. Detailed information on the sampling procedure was provided by Daan & Mulder (2009). The resultant dataset consists of biomass (ash-free dry weight)

and number of individual organisms. Associated abiotic variables were particulate organic matter and carbon (measured from field samples), means of monthly median bottom current speed (m s^{-1}) and bottom wave energy (Pa) (modelled from Deltares Institute, Delft, The Netherlands), depth (European Monitoring Observatory and Data Network 2018) and primary productivity ($\text{mg C m}^2 \text{d}^{-1}$, modelled from Baretta et al. 1995).

2.3.2. Bay of Biscay

The study area ranges between 43.7°N at the northern margin of Gulf of Cap Breton in the south and 48.8°N in the north (Fig. 1b). The slope of the shelf is generally gentle (around 0.5%), and the bottom is dominated by unconsolidated sediments composed mainly of sand and muddy sand, except in a large area in the north and on the continental slope where mud dominates. A total of 523 stations were considered (65 stations on average each year), covering mainly the soft-bottom habitats of the continental shelf (50–200 m), including some stations on the upper slope (200–735 m). In the ongoing French Groundfish Survey in the Celtic Sea and Bay of Biscay (Mahe & Laffargue 1987), a 36/47 Grande Ouverture Verticale trawl is used, with a 20 mm mesh cod-end liner, to sample benthic assemblages. Each haul lasts for approximately 30 min (sampled surface area of about 70000 m^2). To be consistent with available fishing pressure data, we used epibenthic macroinvertebrate data (wet biomass and number of individuals) covering the period from 2009 to 2016. We also selected data deeper than 50 m to reduce the bias due to incomplete effort data for fishing vessels smaller than 12 m long that mainly operate in the shallower areas. Associated abiotic variables include mean annual bottom temperature, mean bottom salinity and the bottom current speed, obtained from the outputs of the MARS 3D model (Lazure & Dumas 2008), sediment characteristics derived from discrete sediment categories (Bouysse 1985, SHOM 2014) and depth recorded during the surveys (Mahe & Laffargue 1987).

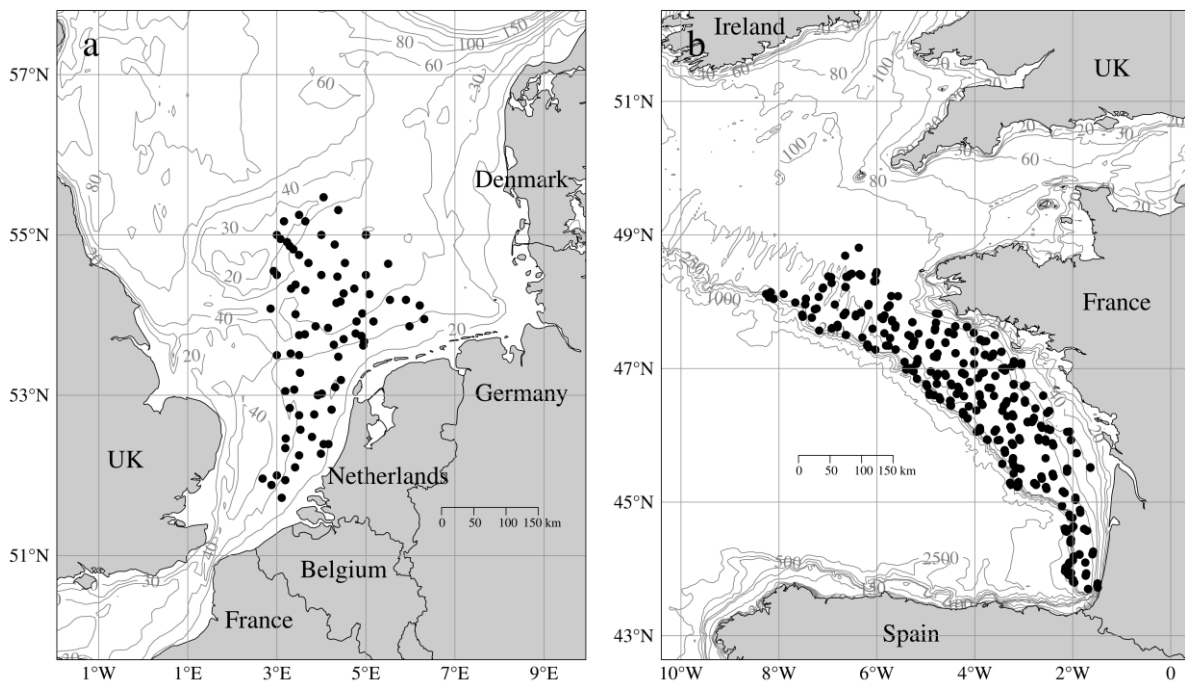


Fig. 1. Case studies. (a) Dutch exclusive economic zone (EEZ), (b) Bay of Biscay. Black dots show sampling stations; grey contours are isobaths displaying depth (m)

2.4. Trawling intensity

In the Dutch EEZ, a large part of the fishery that geographically takes place in the southern North Sea are beam trawls with gear width of 24 m and penetration depths $>2 \text{ cm}$ for a large part of the gear (see Rijnsdorp et al. 2020 and Hintzen et al. 2021 for more details). Shrimp trawls are common all along the Dutch, German and Danish coastlines with a gear of 9 m on either side. Penetration depth in the

sediment is generally shallow due to the light gear used. Commercial fisheries in the Bay of Biscay target various stocks in different ways. Bottom trawlers account for nearly 29% of the fleet (slightly more than 400 vessels). These vessels have an average size of about 15 m and target demersal and benthic species, using mainly bottom otter trawls with a width of about 50 to 100 m between the trawl doors, depending on the size or power of the vessels. A proportion of vessels also use twin trawls for *Nephrops norvegicus*, especially in the northern part. Gear penetration depth is difficult to evaluate due to their disparity.

This study covers the period 2010–2015 for the Dutch EEZ, and the period 2009–2016 for the Bay of Biscay. To estimate fishing pressure, vessel monitoring system (VMS) data in combination with logbook data were used to estimate the surface area fished in between consecutive VMS pings to a specific fishing gear and specific fishing practice (speed-based rule, Poos et al. 2014). The logbooks furthermore provide information on gear width or vessel power that were used to estimate gear width for otter trawls and flyshoot. Fishing effort was quantified as the sum of the area covered by a fishing gear over 1 yr divided by a $0.05^\circ \times 0.05^\circ$ grid cell. This swept area ratio (SAR) was calculated for the year preceding the sampling date in both case studies. In the North Sea study area, trawling intensity was computed according to van Denderen et al. (2015). For the Bay of Biscay, we utilized the surface abrasion dataset computed from the International Council for the Exploration of the Sea (2017b) and the publicly available OSPAR database (Convention for the Protection of the Marine Environment of the North-East Atlantic 2017).

2.5. Data analyses

To test H1, we investigated the relationships between traits and SE and RE components across taxa, using centred principal component analysis (PCA) of the species \times standardised traits matrices from the 2 case studies. The use of traits independently of field data ensured equal weights for vulnerable and resilient or resistant taxa to reflect an ideal non-disturbed pattern. Complementarily, we analysed the distributions of the synthetic SE, RE and vulnerability (SE + RE and SE \times RE) traits that could account for specific benthic signatures such as skewness or multimodality.

To test H2, for each case study, traits were combined with survey data by aggregating organism densities per station and per trait to generate sampling-stations \times response variables matrices (community weighted mean, CWM; for a community, sum of products between taxon densities and taxon trait scores; Kleyer et al. 2012). Prior to calculating CWM, all individual and combined traits within SE and RE were computed in each taxa \times standardised traits matrix, generating 26 response variables, as well as the SE + RE and SE \times RE variables.

Six different types of organism densities were incorporated into stations \times taxa matrices: biomass m^{-2} , number of individuals m^{-2} and number of taxa m^{-2} as absolute values and also as relative values calculated by dividing absolute values by sample totals. The testing of several types of faunal data in the community matrices accounts for the fact that different types of data may be more relevant in different components of the benthos (macrobenthos or megabenthos) sampled using different gears and protocols. Analyses based on different types of data may also inform on different processes within the community. For instance, species biomass provides a more direct measure of resource use than abundance, as energy flow is known to vary with biomass (Valiela 2015). However, absolute densities generally reflect faunal responses along gradients of production, and not necessarily specific functional aspects independent of production. For instance, the use of relative densities is relevant to conservation purposes when functional aspects are given priority over total abundance. Thus, a habitat may be considered vulnerable if it is dominated by vulnerable taxa regardless of their total abundance.

Then, in order to compare the relative effects of abiotic variables and trawling intensity on the CWM traits, we decomposed the variance of each response variable, accounting for the effects of environmental variables and trawling intensity using variation partitioning (Legendre & Legendre 2012). In general, benthic communities are not randomly distributed, and environmental conditions that may benefit or exclude some species may also benefit fishing (e.g. benthic primary productivity; Hintzen et al. 2021). As a consequence, a significant indicator response to trawling can be a spurious effect if an environmental variable is also correlated with the response and is the true explanation of the variation (i.e. a confounding effect). Therefore, to capture the pure trawling effect, response variation to trawling intensity was analysed by partial correlation, after removing the variance of environmental variables

common to response and trawling intensity variables. Variation partitioning proceeds linearly and variables were therefore ln-transformed prior to analysis. For a detailed explanation of the procedure, see an example from the analyses in Supplement 2. Fig. 2 summarises our analytical approach.

Analyses were done with R 4.0.3 (R Core Team 2020); PCA with the package ‘ade4’ (Chessel et al. 2004), and variation partitioning with the package ‘vegan’ (Oksanen et al. 2010).

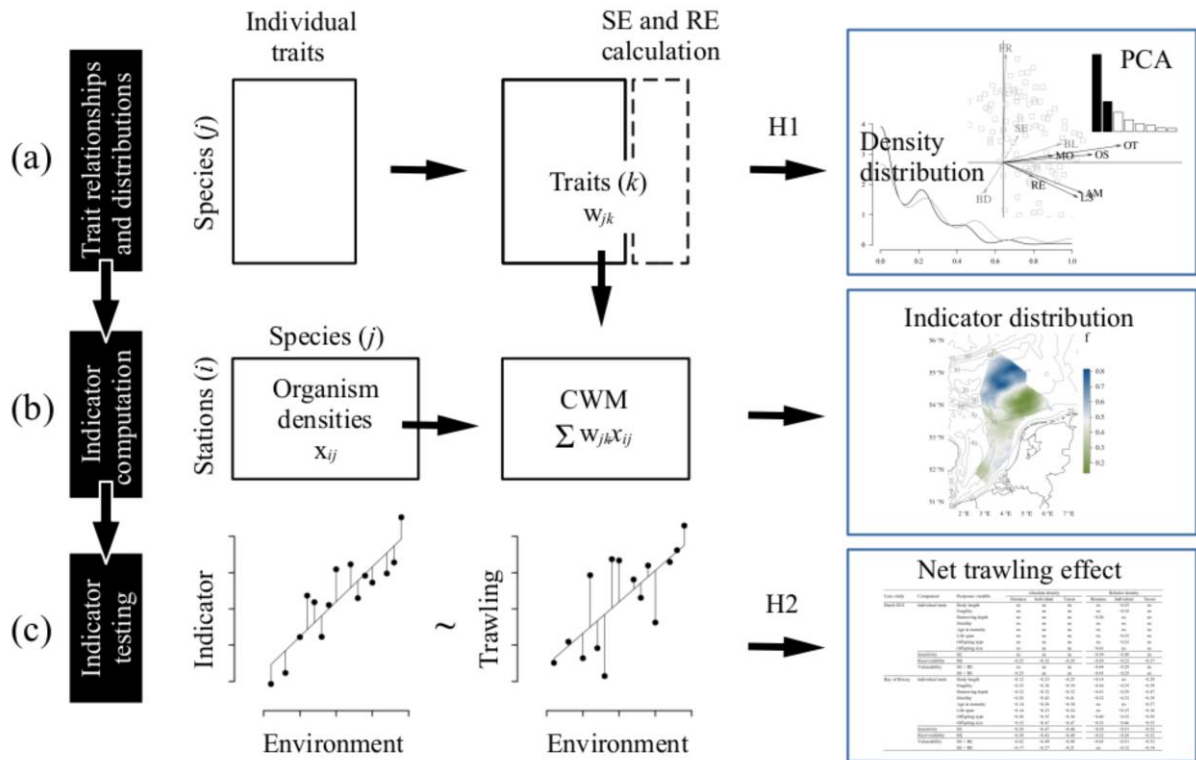


Fig. 2. Summary of data analyses. (a) Sensitivity (SE) and recoverability (RE) components are calculated from the species \times individual traits matrix; PCA and distribution analyses are then used to test hypothesis 1 (H1). (b) Trait data are combined with organism densities from survey data through community weighted means (CWMs), enabling representations of SE and RE spatial distributions. (c) CWM indicator data are then related to observed trawling intensity through variation partitioning; the net trawling influence is derived by the correlation of the residuals from the regressions of indicator and trawling variables on abiotic descriptors (partial correlation), assessing H2

3. RESULTS

3.1. Functional aspects of the studied faunas

Despite differences in geography and sampling methods, the distributions of trait modalities were broadly similar between the 2 faunas (Fig. S3.1 in Supplement 3). As expected, higher proportions of taxa >3 cm body length with shallower burrowing ability were found in the trawls from the Bay of Biscay. To a lesser extent, higher proportions of robust taxa and taxa with larvae of large size were also more characteristic of the Bay of Biscay. Species with short life spans (<1 yr) and dispersing as juveniles were more prevalent in the Dutch EEZ endobenthos.

3.2. Trait relationships

PCA ordinations (Fig. 3) display the relationships between traits for each of the 2 faunas. In both case studies, all recoverability traits covaried positively along the first axis. Adult traits (life span and age at maturity) diverged together from the combination of offspring traits (type and size), motility

keeping an intermediate position. In contrast, sensitivity traits, more expressed along the second axis, were less covariant. Except for body length, traits were more correlated within than between sensitivity and recovery components; correlation matrices are provided in Table S5.1 in Supplement 5. Sensitivity and recoverability components were globally independent as displayed by their orthogonality (Dutch EEZ, $r = 0.02$, $p = 0.768$; Bay of Biscay, $r = 0.13$, $p = 0.102$). Both variables, projected as passive elements, showed similar norms (vector length), indicating that they contributed similarly to biological variations between taxa. This functional independence between sensitivity and recoverability suggests that both components could provide complementary information about short- and longer-term responses to trawling. Therefore, our first hypothesis was supported.

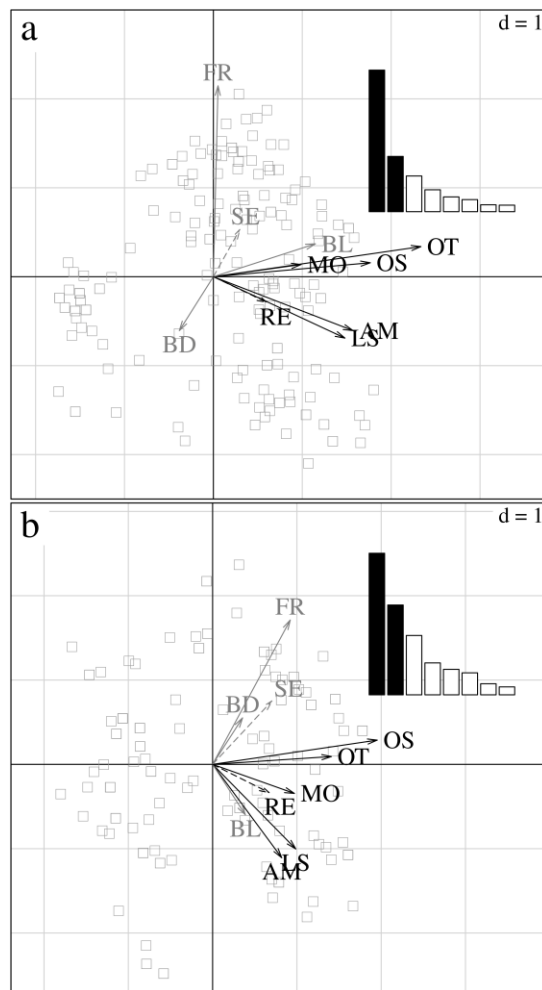


Fig. 3. Principal component analysis of biological trait covariances from taxa \times standardised traits matrices. (a) Endobenthos from the Dutch EEZ. (b) Epibenthos from the Bay of Biscay. Bar diagrams, eigenvalues (black, axes 1 and 2). Grey arrows show traits of the sensitivity (SE) component; black arrows indicate traits of the recovery (RE) component. Dashed arrows, SE and RE components are projected as passive elements. Grey squares represent taxa. ‘d’ indicates the grid scale. AM: age at maturity; BD: burrowing depth; BL: body length; FR: fragility; LS: life span; MO: motility; OS: offspring size; OT: offspring type. Table S4.1 in Supplement 4 provides correlations between traits

3.3. Synthetic trait distributions

The density distributions of sensitivity and recoverability components are shown in Fig. 4, indicating low proportions of sensitive and slow-to-recover taxa in both faunas. Individually, sensitivity and recoverability components of both communities were distributed similarly (Fig. 4a,b). Differences were observed between the 2 variants of vulnerability (SE + RE and SE \times RE), both indicating slightly higher proportions of vulnerable taxa in the Bay of Biscay (Fig. 4c,d).

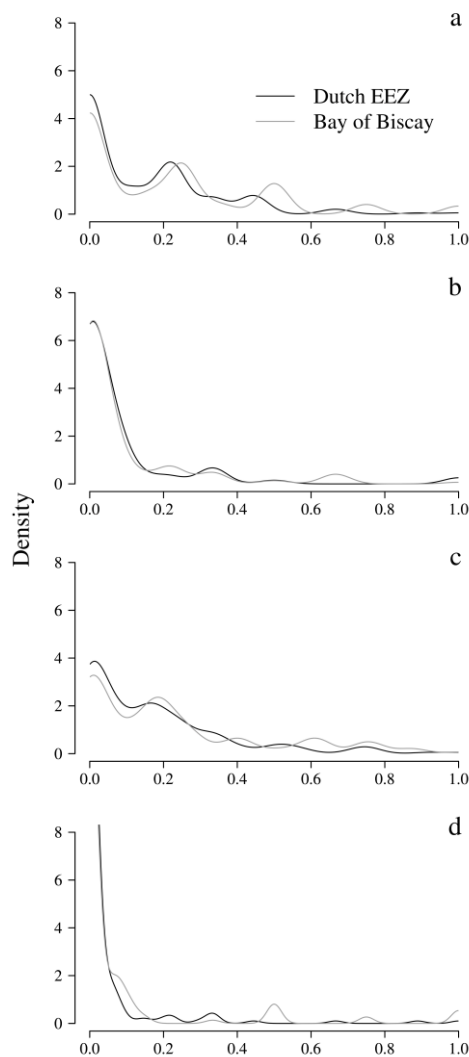


Fig. 4. Density distributions of (a) sensitivity (SE) and (b) recoverability (RE) components, and (c,d) vulnerability ($SE + RE$ and $SE \times RE$, respectively); x-axis, standardised indicator score. As the number of taxa differs between the 2 case studies, data are standardised in order to only compare the shapes of the curves through probability densities. Below-curve area represents the density of taxa

Fragile epibenthic species, including pennatulaceans (e.g. *Funiculina quadrangularis*, *Pteroeides griseum*), *Alcyonium* spp., *Hymenodiscus coronata* and crinoids (*Antedon* sp. and *Leptometra celtica*), were the most sensitive species encountered in the Bay of Biscay. Similarly, fragile species including shallow burrowers *Acrocnida brachiata*, *Amphiura filiformis*, *Eupolyornia nebulosa*, *Phaxas pellucidus*, *Poecilochaetus serpens*, *Psammechinus miliaris*, *Ophiura* sp. and *Spiophanes bombyx* were among the most sensitive taxa in the Dutch EEZ. Conversely, least sensitive taxa were deep burrowers, including the mud shrimps *Callinassa* sp. and *Upogebia deltaura* mostly sampled in the Dutch EEZ, hard-shelled taxa such as *Pagurus bernhardus* found in both study areas and small-bodied taxa including species of the amphipod genus *Bathyporeia*. In the Dutch EEZ, some highly abundant taxa, including *A. brachiata*, *A. filiformis*, *Arctica islandica*, *Brissopsis lyrifera*, *Echinocardium* sp., *Mya* spp., *Pholoe minuta* and *Scoletoma fragilis*, had higher vulnerability scores ($SE + RE$; range 0.25–0.92). In the Bay of Biscay, vulnerability scores among the most abundant taxa were relatively lower, with the exception of the urchin *Gracilechinus acutus* and crinoids (*Antedon* sp. or *Leptometra* sp.) that ranged between 0.5 and 0.6. As expected, vulnerability scores for other abundant species were all below 0.5. Species of pennatulaceans (e.g. *Funiculina quadrangularis*), although relatively less abundant, had the highest vulnerability scores ($RE + SE$, range 0.63–1.00).

3.4. Trawling intensity and confounding effects with environmental variables

Trawling intensity (as SAR) was similarly distributed in both study areas, with low values dominating (Fig. 5a,b). However, the range of SAR values was significantly wider for the Bay of Biscay (25% of SAR values above 4.6) than for the Dutch EEZ (maximal SAR = 4.7). In the Dutch EEZ, trawling intensity was strongly predicted by abiotic variables (trawling intensity regressed on abiotic variables, $R^2 = 0.78$). Most response variables were also strongly predicted by abiotic variables (Table S5.1). Consequently, increasing trawling intensity was inexorably accompanied by an increase in confounded effects of trawling intensity and environmental characteristics. This hampered the detection of true trawling effects on response variables following variation partitioning (Fig. 5c; Table S5.1). A similar trend, although detected (trawling vs. environment, $R^2 = 0.14$), was less pronounced in the Bay of Biscay (Fig. 5d; Table S5.2).

3.5. Trait responses to trawling

The results of our analyses (Table 2) show that, in general, trait combinations were more responsive to trawling intensity than single traits. Therefore, our second hypothesis (H2) was supported. As expected, when significant, all traits responded negatively to trawling, except offspring type and size, especially in the Bay of Biscay. Tables S5.1 & S5.2 display complementary results for different sub-combinations of traits within SE and RE components, including confounding effects.

Table 2. Trait responses to trawling intensity. Values are partial r, Pearson's r-correlation coefficient between trait and trawling intensity after controlling for the effect of abiotic variables (partial regression). EEZ: exclusive economic zone; ns: not significant ($p \geq 0.05$); SE: sensitivity; RE: recoverability

| Case study | Component | Response variable | Absolute density | | | Relative density | | |
|---------------|-------------------|-------------------|------------------|------------|-------|------------------|------------|-------|
| | | | Biomass | Individual | Taxon | Biomass | Individual | Taxon |
| Dutch EEZ | Individual traits | Body length | ns | ns | ns | ns | -0.25 | ns |
| | | Fragility | ns | ns | ns | ns | -0.24 | ns |
| | | Burrowing depth | ns | ns | ns | -0.20 | ns | ns |
| | | Motility | ns | ns | ns | ns | ns | ns |
| | | Age at maturity | ns | ns | ns | ns | ns | ns |
| | | Life span | ns | ns | ns | ns | -0.25 | ns |
| | | Offspring type | ns | ns | ns | ns | -0.23 | ns |
| | | Offspring size | ns | ns | ns | -0.41 | ns | ns |
| | Sensitivity | SE | ns | ns | ns | -0.39 | -0.30 | ns |
| | Recoverability | RE | -0.25 | -0.32 | -0.28 | -0.39 | -0.23 | -0.37 |
| Vulnerability | SE + RE | ns | ns | ns | -0.44 | -0.29 | ns | |
| | SE × RE | -0.25 | ns | ns | -0.43 | -0.25 | ns | |
| Bay of Biscay | Individual traits | Body length | -0.21 | -0.22 | -0.24 | ns | ns | -0.35 |
| | | Fragility | -0.34 | -0.28 | -0.29 | -0.24 | -0.28 | -0.32 |
| | | Burrowing depth | -0.30 | -0.24 | -0.25 | -0.24 | -0.20 | -0.30 |
| | | Motility | -0.32 | -0.34 | -0.35 | -0.25 | -0.29 | -0.31 |
| | | Age at maturity | -0.22 | -0.23 | -0.25 | ns | -0.09 | -0.31 |
| | | Life span | -0.23 | -0.20 | -0.21 | ns | ns | -0.14 |
| | | Offspring type | -0.30 | -0.28 | -0.29 | -0.33 | -0.27 | -0.42 |
| | | Offspring size | -0.35 | -0.38 | -0.39 | -0.29 | -0.38 | -0.41 |
| | Sensitivity | SE | -0.36 | -0.38 | -0.39 | -0.29 | -0.42 | -0.42 |
| | Recoverability | RE | -0.39 | -0.36 | -0.35 | -0.26 | -0.28 | -0.26 |
| Vulnerability | SE + RE | -0.41 | -0.40 | -0.41 | -0.36 | -0.45 | -0.43 | |
| | SE × RE | -0.29 | -0.32 | -0.27 | -0.20 | -0.22 | -0.21 | |

In the Dutch EEZ, relative biomass density was the most responsive to trawling, and not confounded with responses to environmental variables (Table S5.1, adjusted R^2 ranging from 0.02 to 0.15). Overall, individual trait responses were mostly insignificant, except offspring size based on relative biomass. Trait responses were highly obscured by confounding effects of abiotic variables, masking the effect of trawling intensity (Fig. 5c), with limited amounts of explained variance left when controlling for the effect of the environment (Table S5.1). In general, SE was less responsive than RE, in spite of smaller

confounding effects (average adjusted $R^2 = 0.12$ for SE against 0.33 for RE). Whereas all densities returned similar latitudinal contrasts in SE, RE and vulnerability (Figs. S6.1 & S6.2 in Supplement 6; higher values in the north), the main spatial differences between SE and RE components were observed for absolute and relative biomass densities. Vulnerability based on the additive combination of SE and RE for relative biomass responded most strongly (Fig. 6a–c) and SE and RE spatial patterns were the most contrasted with marked local complementarities (Fig. 7a–c).

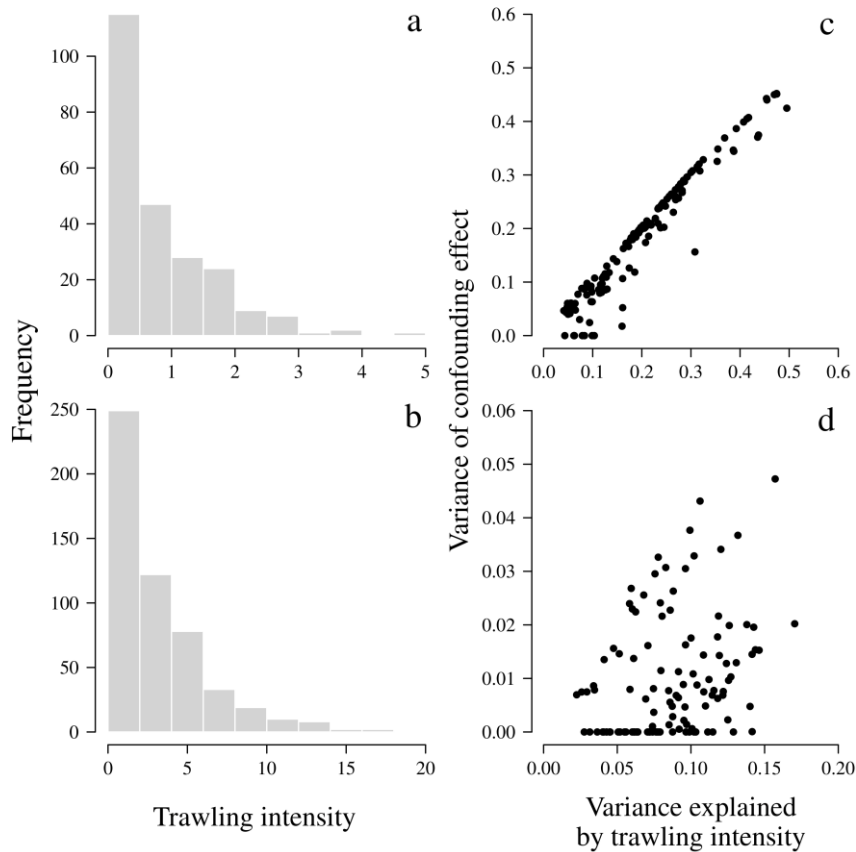


Fig. 5. Frequency distributions of trawling intensities expressed as swept area ratio for (a) the Dutch EEZ and (b) the Bay of Biscay. Also shown is the variance of response variables for individual traits and combinations of traits concurrently explained by abiotic variables and trawling intensity (confounding effect) plotted against variance explained by raw trawling intensity only for (c) the Dutch EEZ and (d) the Bay of Biscay. Each dot refers to a response variable (individual trait or combination of traits) for which the conditional trawling effect was significant (see Tables S5.1 & S5.2 in Supplement 5)

In the Bay of Biscay, the 3 types of densities (and their relative counterparts) responded similarly, with higher partial correlations for relative individual and taxon densities. The spatial distribution of the 2 components corresponded largely to some of the major habitats in the Bay of Biscay (Fig. 7d,e; Figs. S6.3 & S6.4). In addition to smaller confounding effects, explained variances were often higher than in the Dutch EEZ (Tables S5.1 & S5.2). Vulnerability responded most strongly, and this was also the case with the additive combination of SE and RE (Fig. 6d,e). The additive combination of SE and RE, as well as the 2 components separately, showed similar spatial patterns notwithstanding the type of densities. Both components corresponded largely to some of the major habitats in the Bay of Biscay (Fig. 7d,e; Figs. S6.3 & S6.4).

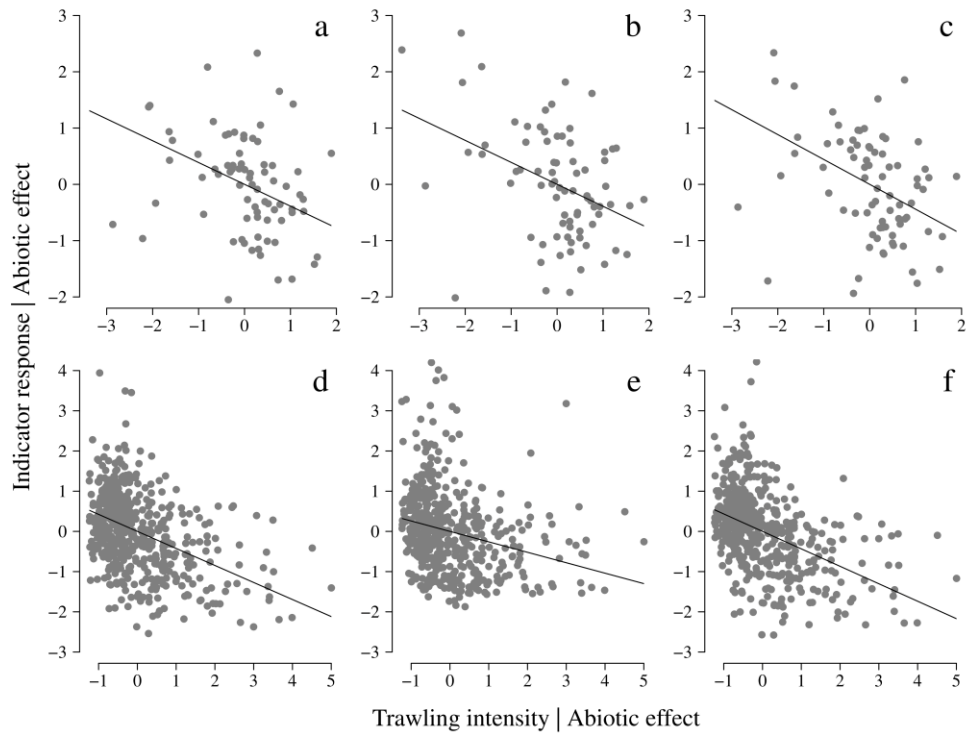


Fig. 6. Strongest indicator responses obtained for each case study. (a–c) Dutch EEZ, relative biomass density; (d–f) Bay of Biscay, relative number of taxa. Variables are standardised residuals from regression on abiotic variables (symbol ‘|’, partial regression). (a,d) Sensitivity. (b,e) Recoverability. (c,f) Vulnerability = Sensitivity + Recoverability

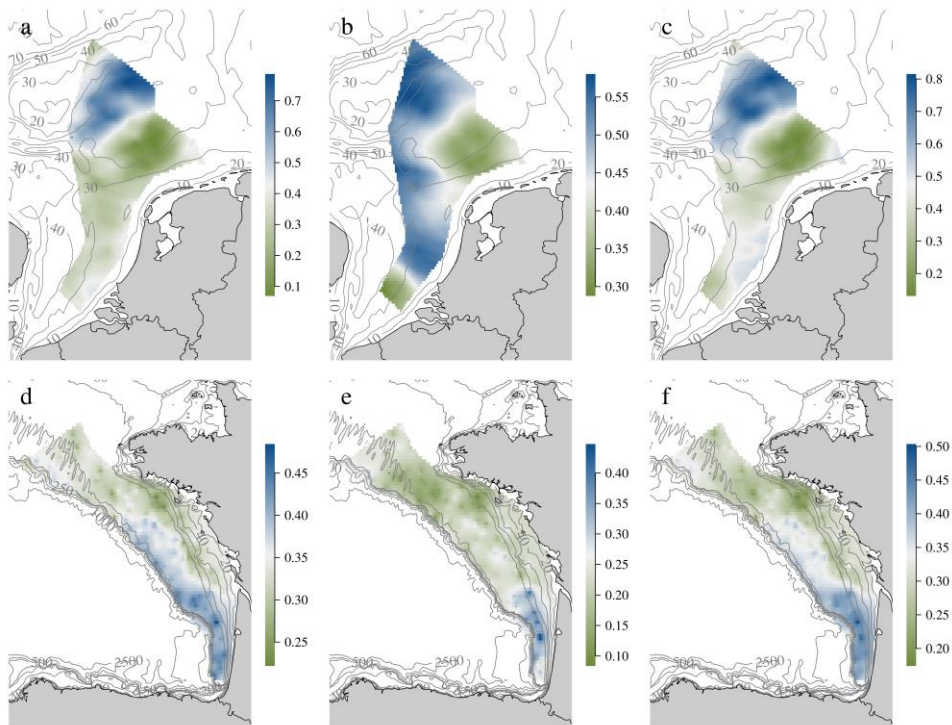


Fig. 7. Interpolation maps of the most responsive variables for (a–c) Dutch EEZ, (d–f) Bay of Biscay. (a,d) Sensitivity (SE), (b,e) recoverability (RE) and (c,f) vulnerability (SE + RE). Values are organism densities multiplied by trait scores, rescaled to the interval [0–1]

4. DISCUSSION

4.1. Responsiveness of benthic community traits to trawling

The response of benthic community traits to trawling was consistent with our expectations. Corroborating the findings of Bolam et al. (2014), our results clearly advocate for the use of multiple traits rather than a single trait in synecological studies. While recent studies proposed life span as the single trait determining the benthic community response (e.g. the ‘longevity approach’, Hiddink et al. 2019, Rijnsdorp et al. 2020), this (1) assumes that the single trait adequately represents the recoverability component (RE) and (2) ignores the sensitivity component (SE). Out of 12 tests (6 densities in each case study), life span was significant only 5 times compared to RE, which was always significant. This supports the contention that densities of long-lived species may lose their indicator potential beyond a certain level of trawling intensity, whereas the alternative, relative maturity (RM), may indicate fishing effects, even at high and prolonged trawling intensities.

In the Dutch EEZ, the lower SE responsiveness may be due to a much higher proportion of buried species compared to purely epibenthic ones. Only 13 taxa with a high (> median) SE score (7% of the total) were epibenthic, against 35 taxa (18%) of deep burrowers (>5 cm). In contrast, 68 taxa with high SE scores (40%) in the Bay of Biscay were epibenthic and none were deep burrowers, probably explaining the regular SE responsiveness there. Significant responses of SE in the Dutch EEZ, only observed for relative biomass and individual densities, may have been due to dominant epibenthic or shallow-dwelling taxa with high SE scores. We cannot provide accurate estimates of trawl mortality as a function of burrowing depth, as no information on gear penetration depth was available, and it is known that the same gear can have different effects in different sediment types (Kaiser et al. 2006). However, 2 reasons support that burrowing depth is likely a driving characteristic of vulnerability, especially in the Bay of Biscay. Firstly, Tianio et al. (2020) experimentally compared the effects of 2 contrasting trawling techniques (pulse and tickler chain trawls; both in soft mud) on benthic fauna; as expected, epibenthic and shallow burrower densities were depleted, but no significant difference was detected between the 2 trawling techniques. Secondly, a larger proportion of the fauna from the Bay of Biscay was epibenthic (Fig. S3; almost 70% of the taxa, compared to less than 15% in the Dutch EEZ) and was likely more exposed to trawling gears than the fauna from the Dutch EEZ, where >35% of the taxa could be found >5 cm deep (cf <10% in the Bay of Biscay). Comparatively, the usual penetration depths of bottom trawls rarely exceed 5–10 cm (Eigaard et al. 2016).

Our analyses using biomass densities of endobenthos in the Dutch EEZ recorded a large area of low sensitivity centred on the Frisian Front (Fig. 7a–c, around 54° N). There, the very deep burrowers *Callianassa* sp. and *Upogebia deltaura* comprise a large proportion of total benthic biomass. In contrast, vulnerability based on number of taxa is higher in this area due to high SE and/or RE scores of many species with relatively low biomass densities (Fig. S6.1i–k). In the Bay of Biscay, the continental shelf encompasses a patchwork of habitats, resulting in different processes driving apparently similarly low SE values. In the north-eastern part (Fig. 7d, 45.5–46.5° N), a muddy area named ‘Grande Vasière’, low SE values result from the dominance of burrowing organisms and the presence of the most sensitive epibenthic species with densities greatly reduced by intensive fishing in that area over several decades. In the sandy habitats of the transitional area between the Celtic Sea and the Bay of Biscay (around 47.5° N), low SE values reflect high biomass of some trawling-resistant species including the anemone *Actinauge* sp. and the paguroid *Pagurus prideaux*. Highest SE values in the southernmost areas were mainly due to the dominance of sensitive species including pennatulaceans (*Pteroeides* spp. or *Funiculina* spp.) and crinoids (*Leptometra celtica*). The latter species is also found in patches in the central area of the Bay of Biscay between the 100 m isobath and the shelf-break where high SE values were also recorded.

For benthic community status assessments, the choice of biomass, individual or taxon densities may be determined by the focus of the assessment. For example, trawling effects on biodiversity might best be assessed using taxon densities. Conversely, effects on foodweb functioning would be more meaningfully established based on biomass, and individual density may be less appropriate (as it is biased towards representing the most abundant species) for expressing multi-faceted and often ill-defined concepts such as community health or seafloor integrity (as used in the Marine Strategy

Framework Directive). In the Dutch EEZ, stronger relationships for traits weighted by biomass were found than for traits weighted by individual or taxon densities, especially when relative densities were applied. High biomass densities can indicate the presence of old individuals of vulnerable species (i.e. those requiring sufficient time without disturbance to ensure reproductive success), whereas high numbers of individuals can simply reflect high numbers of young vulnerable organisms at the beginning of a recovery period or high numbers of resilient smaller and shorter-lived organisms, as evidenced by abundance-biomass comparisons along successions in the marine benthos (Pearson & Rosenberg 1978, Warwick & Clarke 1994, Diaz & Rosenberg 1995). In the Bay of Biscay, the consistent responsiveness among the different types of densities may be explained by steeper species richness gradients compared to other densities (Figs. S6.3 & S6.4), coupled with the negligible confounding effects of environmental variables in this area (see Section 4.2).

4.2. Confounding effects

The strong confounding environmental effects encountered in the Dutch EEZ were probably responsible for the absence of significant responses for many variables, as explained variances were of similar magnitudes (Table S5.1). Consequently, removing the confounding effect from the total effect left only small amounts of variance in the benthic community traits to be explained by trawling intensity. In the Dutch EEZ, trawling intensity increases from the deeper water in the north to the shallow water in the south, as does primary productivity (correlated to trawling intensity, $r = 0.66$, $p < 0.001$), so that it is difficult to appraise the true trawling effect on what is effectively a correlated gradient. The response of benthic communities could therefore be the result of an increase in trawling intensity, a change in habitat, or both. This was also observed for species richness by Duineveld et al. (1992). In our study, this is demonstrated by the generally high level of variance in abiotic variables (Table S5.1). Besides, opposing directions of change in trawling intensity and a given indicator could mask the effects of trawling disturbance buffered by environmental suitability (i.e. compensating depletion). As observed in the Dutch EEZ, the use of relative densities may, to some extent, mitigate the confounding effect of production gradients by emphasising the functional nature of communities more compared to analyses based on species richness or total organism density (Beauchard et al. 2017).

Few benthic studies have explicitly taken confounding effects into account (Lindgarth et al. 2000, Hinz et al. 2009, Reiss et al. 2009, Jac et al. 2020). To our knowledge, no work developing composite trait indicators has sought to statistically validate this important aspect. Several studies were previously carried out along gradients of commercial fishing intensity, some of which probably involved correlations with other forms of anthropogenic physical disturbance and, importantly, environmental variability. The conclusions drawn from such studies should be considered with caution. Variation in fishing intensity often follows variation in fish abundance and habitat suitability, both of which are driven by variation in the environment (Pommer et al. 2016). To truly disentangle fishing effects, long-term fishing exclusion from different habitats (i.e. those with different degrees of vulnerability) would offer better experimental contexts (Hall 1999, Gray et al. 2006).

4.3. Developing a trait-based vulnerability indicator

Here, we present a generic approach that can be used to develop a trait-based indicator to assess the vulnerability of benthic communities to fishing-induced physical disturbance. This approach is based on 2 processes derived from a mechanistic understanding of trawling effects on the benthic community, i.e. sensitivity and recoverability, and is well-grounded in benthic ecological theories. We chose to offer a generic approach so that it can be adjusted to fit specific contexts in terms of data availability, knowledge of the benthic fauna and traits selected to express both SE and RE processes. As trait scores take the value 0 in species that are not vulnerable, null scores of combined variables are likely to increase with more traits, leading to a larger number of species that do not contribute to the community score. This ensures that non-null scores arise from vulnerable species which are not resistant and with limited resilience. In areas where benthic communities are extremely impoverished, it may be necessary to limit the number of traits considered, in order to minimise the number of null scores. However, in the case of correlated traits such as in the RE component, the number of null scores of combined variables is limited as vulnerable species have high scores for most of the traits. Conversely, the use of the SE component

may be more conservative for the detection of trawling effects, given the strong independence of SE traits.

Further work, using data collected under controlled conditions, is recommended before deciding on a definitive version of an indicator combining both SE and RE components. Indeed, there may not be a single 'best' vulnerability indicator but a range of similar ones that are tailored to the benthic community being studied, how it was sampled and the overall local conditions. For example, a benthic community not impacted by trawling previously, would be characterised by a large spread of SE and RE scores due to higher proportions of vulnerable species. When trawling commences, the relative contributions of SE and RE components to the decreasing vulnerability indicator are expected to change over time, i.e. first dominated by the SE and later by the RE component. After the initial trawl pass, it can reasonably be assumed that the first responding individuals/species will be those with higher SE scores (e.g. sea pens). Then, under continued and frequent trawling that does not allow recovery, only species with sufficient resilience relative to trawling intensity will survive continued trawling, so the SE score remains low. Once fishing ceases, indicator response is determined, chronologically, by the SE component, followed by the RE component dominated initially by high relative maturity (RM) scores and later by life span. After implementation of a marine protected area, for example, the indicator responsiveness would be determined in the short term by SE and in the long term by RE. In our case study areas, both of which involved trawled communities, SE responses may be considerably smaller than what might have been expected under pristine, or at least less degraded, circumstances. As such, both SE and RE need to be included in a benthic vulnerability indicator that is expected to perform well under very different circumstances.

The range of variation in trawling intensity was large enough in our study to detect significant responses of some trait-based indicator components. However, the general lack of responsiveness of life span, an important recoverability trait, may be explained in both case studies by temporal contingencies. In both areas, the presence of species with potentially high scores for both SE and RE was observed long ago (Houziaux et al. 2011). The long history of sustained bottom trawling may have extirpated a substantial proportion of the vulnerable epibenthic fauna. Bottom trawling is known to have affected European coastal areas since the 13th century (de Groot 1984), expanding to further and deeper areas in the following centuries (Joubin 1922). The resulting lack of lightly impacted areas, and hence a limited variation in SE, RE and vulnerability among both endo- and epibenthic communities, may have masked greater RE responsiveness. Nevertheless, we cannot exclude some limitations from our spatial sampling resolution to properly detect local patches of vulnerable epibenthic fauna as evidenced by the recent discovery of a *Sabellaria spinulosa* reef in an area of intense demersal fishing within the Dutch EEZ (van der Reijden et al. 2019).

Lastly, the inclusion of other important traits could have enhanced the performance of our approach. In the SE component, body regeneration could have been relevant, but its documentation remains questionable for many species such as bivalves exposing their siphons to predators or regenerating shell. Also, as illustrated by the noticeable responsiveness of offspring type and size, offspring traits should deserve more attention. Besides, information on larval settlement cues could have improved the RE component. Different species with differing growth rates and life spans require cues for settling, such as the presence of adults or aspects of the physico-chemical nature of the sea floor (Pechenik 1990, Pawlik 1992). Given the effects of bottom trawling on the sediment (Schwinghamer et al. 1998), larval settlement is likely to be impaired by removing adults or by altering the nature of the sediment.

4.4. Conclusions

Based on a theoretically sound mechanistic understanding of trawling effects on the benthic community, this study advocates the use of multiple biological traits for assessing the status of seabed habitats specifically in relation to trawling-induced physical disturbance. We emphasise the complementarity of SE and RE components and their relative importance depending on the study context. In this study, their independence is a major finding, implying that vulnerability cannot be fully understood using a single trait or several ones only reflecting the intrinsic rate of natural increase. Our results show that an assessment of the status of seabed habitats, and how these are affected by physical disturbance, requires the full consideration of the benthic community, including both endo- and epibenthic components, each needing different sampling techniques.

Our generic approach to the development of a benthic community vulnerability indicator can be adapted to specific contexts. Depending on the availability of data from monitoring programmes, such as type of fauna sampled (endo- or epibenthos), faunal data recorded (numbers, biomass) and traits were distinguished, an indicator can be created that is likely to perform well even in areas with a long history of exploitation.

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LITERATURE CITED

- Baretta JW, Ebenhöh W, Ruurdij P (1995) The European regional seas ecosystem model, a complex marine ecosystem model. *Neth J Sea Res* 33:233–246 doi:10.1016/0077-7579(95)90047-0
- 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 doi:10.1016/j.ecolind.2017.01.011
- Bergman MJN, van Santbrink JW (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *ICES J Mar Sci* 57:1321–1331 doi:10.1006/jmsc.2000.0917
- Bitschofsky F, Forster S, Scholz J (2011) Regional and temporal changes in epizoobiontic bryozoan-communities of *Flustra foliacea* (Linnaeus, 1758) and implications for North Sea ecology. *Estuar Coast Shelf Sci* 91:423–433
- Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. *J Sea Res* 85:162–177 doi:10.1016/j.seares.2013.05.003
- Bouysse P (1985) Carte des sédiments superficiels du plateau continental du Golfe de Gascogne – Partie septentrionale au 1/500000. BRGM & IFREMER
- Charnov EL (1993) Life history invariants. Some explorations of symmetry in evolutionary ecology. Oxford University Press
- Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package – I – One-table methods. *R News* 4:5–10
- Convention for the Protection of the Marine Environment of the North-East Atlantic (2017) OSPAR data and information management. https://odims.ospar.org/layers/geonode:ospar_bottom_f_intensur_2009_01_002
- Daan R, Mulder M (2009) Monitoring the invertebrate benthic fauna in the Dutch sector of the North Sea 1991–2005: an overview. Rep 2009-5. NIOZ
- de Groot SJ (1984) The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Coast Manag* 9:177–190 doi:10.1016/0302-184X(84)90002-7
- de Juan S, Demestre M (2012) A trawl disturbance indicator to quantify large scale fishing impact on benthic ecosystems. *Ecol Indic* 18:183–190 doi:10.1016/j.ecolind.2011.11.020
- de Juan S, Hinz H, Sartor P, Vitale S and others (2020) Vulnerability of demersal fish assemblages to trawling activities: a traits-based index. *Front Mar Sci* 7:44
- Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural response of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–303

- 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
- Eigaard OR, Bastardie F, Breen M, Dinesen GE and others (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73(Suppl 1):i27–i43 doi:10.1093/icesjms/fsv099
- European Monitoring Observatory and Data Network (2016) Bathymetry – understanding the topography of the European seas. <http://doi.org/10.12770/c7b53704-999d-4721-b1a3-04ec60c87238>
- Foveau A, Vaz S, Desroy N, Kostylev VE (2017) Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. *PLOS ONE* 12:e0184486 PubMed
- Gan X, Fernandez IC, Guo J, Wilson M, Zhaoe Y, Zhou B, Wu J (2017) When to use what: methods for weighting and aggregating sustainability indicators. *Ecol Indic* 81:491–502 doi:10.1016/j.ecolind.2017.05.068
- Giangrande A (1997) Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanogr Mar Biol Annu Rev* 35:323–386
- 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
- González-Irusta JM, De la Torriente A, Punzón A, Blanco M, Serrano A (2018) Determining and mapping species sensitivity to trawling impacts: the Benthos Sensitivity Index to Trawling Operations (BESITO). *ICES J Mar Sci* 75:1710–1721 doi:10.1093/icesjms/fsy030
- Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. *Mar Pollut Bull* 52:840–843 PubMed doi:10.1016/j.marpolbul.2006.07.003
- Hall SJ (1999) *The effects of fishing on marine ecosystems and communities*. Blackwell Science
- Hiddink JG, Jennings S, Sciberras M, Szostek CL and others (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. *Proc Natl Acad Sci USA* 114:8301–8306 PubMed doi:10.1073/pnas.1618858114
- Hiddink JG, Jennings S, Sciberras M, Bolam SG and others (2019) Assessing bottom trawling impacts based on the longevity of benthic invertebrates. *J Appl Ecol* 56:1075–1084 doi:10.1111/1365-2664.13278
- Hintzen N, Aerts G, Poos JJ, Van der Reijden KJ, Rijnsdorp AD (2021) Quantifying habitat preference of bottom trawling gear. *ICES J Mar Sci* 78:172–184 doi:10.1093/icesjms/fsaa207
- Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: chronic effects and experimental predictions. *Ecol Appl* 19:761–773 PubMed doi:10.1890/08-0351.1
- Hinz H, Törnroos A, de Juan S (2021) Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. *Ecol Ind* 126:107692 doi:10.1016/j.ecolind.2021.107692
- Houziaux JS, Fettweis M, Francken F, Van Lancker V (2011) Historic (1900) seafloor composition in the Belgian–Dutch part of the North Sea: a reconstruction based on calibrated visual sediment descriptions. *Cont Shelf Res* 31:1043–1056 doi:10.1016/j.csr.2011.03.010
- International Council for the Exploration of the Sea (2017a) Report of the Workshop to evaluate regional benthic pressure and impact indicator(s) from bottom fishing (WKBENTH). 28 February – 3 March 2017, Copenhagen, Denmark. ICES CM 2017/ACOM
- International Council for the Exploration of the Sea (2017b) Spatial data layers of fishing intensity/pressure per gear type for surface and subsurface abrasion, for the years 2009 to 2016 in the OSPAR regions (ver2, 22 January, 2019): ICES data product release. <https://doi.org/10.17895/ices.data.4685>
- Jac C, Desroy N, Certain G, Foveau A, Labrune C, Vaz S (2020) Detecting adverse effect on seabed integrity. Part 1: Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna. *Ecol Indic* 117:106631 doi:10.1016/j.ecolind.2020.106631
- Joubin ML (1922) *Les coraux de mer profonde nuisibles aux chalutiers*. Notes et Mémoires 18. Office Scientifique et Techniques des Pêches Maritimes, Paris
- Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14 doi:10.3354/meps311001
- Kindsvater HK, Mangel M, Reynolds JD, Dulvy NK (2016) Ten principles from evolutionary ecology essential for effective marine conservation. *Ecol Evol* 6:2125–2138 PubMed doi:10.1002/ece3.2012

- Kleyer M, Dray S, de Bello F, Lepš J and others (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *J Veg Sci* 23:805–821 doi:10.1111/j.1654-1103.2012.01402.x
- Lazure P, Dumas F (2008) An external–internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). *Adv Water Resour* 31:233–250 doi:10.1016/j.advwatres.2007.06.010
- Legendre P, Legendre L (2012) *Numerical ecology*, 3rd edn. Elsevier
- Lindegarth M, Valentinsson D, Hansson M, Ulmestrand M (2000) Interpreting large-scale experiments on effects of trawling on benthic fauna: an empirical test of the potential effects of spatial confounding in experiments without replicated control and trawled areas. *J Exp Mar Biol Ecol* 245:155–169 PubMed doi:10.1016/S0022-0981(99)00158-6
- MacDonald DS, Little M, Eno NC, Hiscock K (1996) Disturbance of benthic species by fishing activities: a sensitivity index. *Aquat Conserv* 6:257–268 doi:10.1002/(SICI)1099-0755(199612)6:4<257::AID-AQC194>3.0.CO;2-7
- Mahe JC, Laffargue P (1987) EVHOE – EVAluation Halieutique Ouest de l’Europe. <https://doi.org/10.18142/8>
- Marine Ecosystem Research Programme (2021) *Marine Ecosystem Research Programme Trait Explorer*. https://www.marine-ecosystems.org.uk/Trait_Explorer
- Mérillet L, Mouchet M, Robert M, Salaün M, Schuck L, Vaz S, Kopp D (2018) Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay). *Environ Conserv* 45:163–172 doi:10.1017/S0376892917000480
- MyOcean (2015) MyOcean project, funded by HORIZON 2020 (EU Research and Innovation programme 2014–2020). <http://www.myocean.eu>
- Oksanen J, Blanchet G, Kindt R, Legendre P and others (2010) *Vegan: community ecology package*. R package version 2.5-3. <http://cran.r-project.org/package=vegan>
- Pawlik JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr Mar Biol Annu Rev* 30:273–335
- 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 doi:10.1080/00785236.1990.10422025
- Pechenik JA (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar Ecol Prog Ser* 177:269–297 doi:10.3354/meps177269
- Pitcher CR, Ellis N, Jennings S, Hiddink JG and others (2017) Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. *Methods Ecol Evol* 8:472–480 doi:10.1111/2041-210X.12705
- Pommer CD, Olesen M, Hansen JLS (2016) Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Mar Ecol Prog Ser* 548:47–60 doi:10.3354/meps11649
- R Core Team (2020) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Reiss H, Greenstreet SPR, Sieben K, Ehrich S and others (2009) Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. *Mar Ecol Prog Ser* 394:201–213 doi:10.3354/meps08243
- Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecol Appl* 28:1302–1312 PubMed doi:10.1002/eap.1731
- Rijnsdorp AD, Hiddink JG, van Denderen PD, Hintzen NT and others (2020) Different bottom trawl fisheries have a differential impact on the status of the North Sea seafloor habitats. *ICES J Mar Sci* 77:1772–1786 doi:10.1093/icesjms/fsaa050
- Schwinghamer P, Gordon DC, Rowell TW, Prena J, McKeown DL, Sonnichsen G, Guigné JY (1998) Effects of experimental otter trawling on surficial sediment properties of a sandy-bottom ecosystem on the Grand Banks of Newfoundland. *Conserv Biol* 12:1215–1222 doi:10.1046/j.1523-1739.1998.0120061215.x
- Sciberras M, Hiddink JG, Jennings S, Szostek CL and others (2018) Response of benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish Fish* 19:698–715 doi:10.1111/faf.12283

- SHOM (Service hydrographique et océanographique de la marine) (2014) Information géographique maritime et littorale de référence. <https://datashom.fr>
- Tiano JC, van der Reijden KJ, O'Flynn S, Beauchard O and others (2020) Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. *Mar Environ Res* 159:104964 PubMed doi:10.1016/j.marenvres.2020.104964
- Tyler-Walters H, Roger SI, Marshall CE, Hiscock K (2009) A method to assess the sensitivity of sedimentary communities to fishing activities. *Aquat Conserv* 19:285–300 doi:10.1002/aqc.965
- Valiela I (2015) *Marine ecological processes*, 3rd edn. Springer-Verlag
- van Denderen PD, Hintzen NT, van Kooten T, Rijnsdorp AD (2015) Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. *ICES J Mar Sci* 72:952–961 doi:10.1093/icesjms/fsu183
- van der Reijden KJ, Koop L, O'Flynn S, Garcia S and others (2019) Discovery of Sabellaria spinulosa reefs in an intensively fished area of the Dutch Continental Shelf, North Sea. *J Sea Res* 144:85–94 doi:10.1016/j.seares.2018.11.008
- Warwick RM, Clarke KR (1994) Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. *Mar Biol* 118:739–744 doi:10.1007/BF00347523

Supplement S1

Table S1.1. Biological traits. Abbreviations: BL, body length; FR, fragility; BD, burrowing depth; MO, motility; AM, age at maturity; LS, life span; OT, offspring type; OS, offspring size; CS, case study (1, Dutch EEZ; 2, Bay of Biscay). See Table 1 for code attributions. References are listed below.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|------------------------------------|----|----|----|----|----|----|----|----|-----|------------------------------------|
| <i>Abludomelita obtusata</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 51,162,230,521 |
| <i>Abra alba</i> | 2 | 3 | 2 | 2 | 1 | 2 | 3 | 4 | 1 | 124,129,290 |
| <i>Abra nitida</i> | 2 | 3 | 3 | 2 | 1 | 2 | 3 | 4 | 1 | 60,129,523 |
| <i>Abra prismatica</i> | 2 | 3 | 3 | 2 | 2 | 2 | 3 | 4 | 1 | 124,129,159,320 |
| <i>Abra tenuis</i> | 2 | 3 | 3 | 2 | 1 | 2 | 3 | 3 | 1 | 129,134,249,290 |
| <i>Acanthocardia</i> sp. | 3 | 1 | 3 | 2 | 2 | 4 | 3 | 4 | 1 | 129,190,319,386 |
| <i>Acrocrida brachiata</i> | 5 | 3 | 2 | 2 | 3 | 3 | 3 | 3 | 1 | 53,54,179,316,319,320 |
| <i>Acteon tornatilis</i> | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 4 | 1 | 129,186,541,542 |
| <i>Actinauge</i> sp. | 3 | 1 | 3 | 4 | 3 | 4 | 3 | 3 | 2 | 337 |
| <i>Aequipecten opercularis</i> | 3 | 1 | 4 | 1 | 2 | 3 | 3 | 4 | 2 | 55,57,320,396 |
| <i>Alcyonium digitatum</i> | 5 | 2 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 227,228,244,339,468 |
| <i>Alcyonium glomeratum</i> | 5 | 2 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 193,227,228,244,339,468,478,479 |
| <i>Alitta virens</i> | 5 | 3 | 1 | 1 | 2 | 2 | 3 | 3 | 1 | 179,278,375 |
| <i>Alpheus glaber</i> | 3 | 2 | 4 | 1 | 1 | 2 | 2 | 2 | 2 | 271,350,385,390,420 |
| <i>Ampelisca brevicornis</i> | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 105,122,320 |
| <i>Ampelisca diadema</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 105,190,266,319,322,355 |
| <i>Ampelisca macrocephala</i> | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 266,322 |
| <i>Ampelisca spinipes</i> | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 266,319,322,417,428,537 |
| <i>Ampelisca tenuicornis</i> | 1 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 322,455,489,509 |
| <i>Ampharete</i> sp. | 3 | 3 | 2 | 3 | 1 | 1 | 3 | 3 | 1 | 125,199,319,322,402 |
| <i>Amphipholis squamata</i> | 3 | 3 | 4 | 2 | 2 | 2 | 1 | 1 | 1 | 155,263,322 |
| <i>Amphiura chiajei</i> | 5 | 3 | 2 | 2 | 3 | 4 | 3 | 3 | 1 | 240,351 |
| <i>Amphiura filiformis</i> | 5 | 3 | 3 | 2 | 3 | 4 | 3 | 4 | 1 | 52,62,352,509 |
| <i>Anseropoda placenta</i> | 4 | 2 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 230,337 |
| <i>Antedon</i> sp. | 5 | 3 | 4 | 1 | 2 | 2 | 3 | 3 | 2 | 26,141,230,282,285,286,303,325,358 |
| <i>Antedon petasus</i> | 5 | 3 | 4 | 1 | 2 | 2 | 3 | 3 | 2 | 26,141,230,282,285,286,303,325,358 |
| <i>Aonides paucibranchiata</i> | 2 | 3 | 3 | 2 | 1 | 1 | 3 | 3 | 1 | 170,190,319,320,530 |
| <i>Aphelochaeta marioni</i> | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 125,167,202,203 |
| <i>Aphrodita</i> sp. | 4 | 2 | 3 | 2 | 2 | 3 | 3 | 4 | 1 | 75,179,190,319,522 |
| <i>Aphrodita aculeata</i> | 4 | 2 | 3 | 2 | 2 | 3 | 3 | 4 | 2 | 75,179,190,319,522 |
| <i>Aporrhais pespelecani</i> | 3 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 1,2 | 129,297,322,388 |
| <i>Aporrhais serresianus</i> | 3 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 129,297,322,388 |
| <i>Arcopagia crassa</i> | 3 | 1 | 2 | 2 | 2 | 3 | 3 | 4 | 1 | 129,190,488 |
| <i>Arctica islandica</i> | 4 | 1 | 3 | 4 | 3 | 4 | 3 | 4 | 1 | 69,129,348,416,487 |
| <i>Aristaeomorpha foliacea</i> | 4 | 1 | 4 | 1 | 2 | 3 | 3 | 3 | 2 | 112,172,230,378 |
| <i>Armina loveni</i> | 2 | 2 | 3 | 2 | 1 | 1 | 3 | 3 | 2 | 160 |
| <i>Asbjornsenia pygmaea</i> | 1 | 1 | 3 | 2 | 2 | 3 | 3 | 4 | 1 | 129,190,319 |
| <i>Astarte montagui</i> | 2 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 1 | 129,430,450 |
| <i>Astarte sulcata</i> | 2 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 129,430,450 |
| <i>Asterias</i> sp. | 5 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 1 | 50,179,512 |
| <i>Asterias rubens</i> | 4 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 50,179,512 |
| <i>Astropecten</i> sp. | 3 | 2 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 179,185,209,322 |
| <i>Astropecten irregularis</i> | 4 | 2 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 179,185,209,322 |
| <i>Atelecyclus</i> sp. | 3 | 2 | 3 | 2 | 2 | 3 | 2 | 1 | 2 | 230,337 |
| <i>Atelecyclus rotundatus</i> | 3 | 2 | 3 | 2 | 2 | 3 | 2 | 1 | 2 | 230,337 |
| <i>Atelecyclus undecimdentatus</i> | 3 | 2 | 3 | 2 | 2 | 3 | 2 | 1 | 2 | 230,337 |
| <i>Atlantopandalus propinquus</i> | 4 | 2 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 230,337 |
| <i>Atrina pectinata</i> | 5 | 1 | 4 | 4 | 2 | 3 | 3 | 4 | 2 | 89,401,405,427,544 |
| <i>Balanus crenatus</i> | 2 | 1 | 4 | 4 | 1 | 2 | 2 | 3 | 1 | 27,404,407 |
| <i>Bathyporeia elegans</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 176,177,243,322,361 |
| <i>Bathyporeia gracilis</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 114,177,190,320,361 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|------------------------------------|----|----|----|----|----|----|----|----|-----|--|
| <i>Bathyporeia guilliamsoniana</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 114,176,177,243,361 |
| <i>Bathyporeia pelagica</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 114,176,177,361 |
| <i>Bathyporeia sarsi</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 114,190,361,510 |
| <i>Bathyporeia tenuipes</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 114,177,239,319,361 |
| <i>Bela nebula</i> | 2 | 1 | 3 | 2 | 1 | 2 | 3 | 3 | 1 | 129,135 |
| <i>Bodotria arenosa</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 261,264,322,454,539 |
| <i>Bodotria scorpioides</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 261,264,319,322,454,539 |
| <i>Branchiostoma lanceolatum</i> | 3 | 2 | 3 | 1 | 2 | 3 | 3 | 3 | 1 | 36,139,238,293 |
| <i>Brissopsis lyrifera</i> | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 4 | 1,2 | 64,173,230,239 |
| <i>Buccinum humphreysianum</i> | 3 | 1 | 4 | 2 | 3 | 4 | 3 | 3 | 2 | 66,129,251,252,253,269,270,323,343 |
| <i>Buccinum undatum</i> | 3 | 1 | 4 | 2 | 3 | 4 | 3 | 3 | 1,2 | 129,269,270,323 |
| <i>Bylgides sarsi</i> | 2 | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 1 | 3,322,438 |
| <i>Calliactis parasitica</i> | 3 | 1 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 179,230,337 |
| <i>Callianassa</i> sp. | 3 | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 243,280,423,424 |
| <i>Calliostoma granulatum</i> | 3 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 179,230,337 |
| <i>Calocaris macandreae</i> | 3 | 2 | 1 | 1 | 2 | 3 | 3 | 2 | 2 | 61,230,356 |
| <i>Cancer bellianus</i> | 5 | 1 | 3 | 2 | 2 | 3 | 2 | 2 | 2 | 34,39,40,71,78,179,230,248,322,331,411,415,439,457,493,517,535,538 |
| <i>Cancer pagurus</i> | 5 | 1 | 1 | 2 | 3 | 4 | 2 | 1 | 2 | 34,40,179,322,535 |
| <i>Capitella capitata</i> | 3 | 3 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 4,46,243,336 |
| <i>Carcinus maenas</i> | 3 | 3 | 3 | 2 | 2 | 3 | 2 | 1 | 1 | 35,179,322,342 |
| <i>Caryophyllia</i> sp. | 2 | 3 | 4 | 4 | 2 | 4 | 3 | 3 | 2 | 179,230,337 |
| <i>Caryophyllia smithii</i> | 2 | 3 | 4 | 4 | 2 | 4 | 3 | 3 | 2 | 179,230,337 |
| <i>Chaetopterus variopedatus</i> | 5 | 3 | 1 | 3 | 1 | 2 | 3 | 3 | 1 | 149,156,230,485 |
| <i>Chaetozone setosa</i> | 2 | 3 | 2 | 2 | 1 | 2 | 3 | 3 | 1 | 88,230,237,243,319,376 |
| <i>Chamelea striatula</i> | 3 | 1 | 3 | 2 | 2 | 4 | 3 | 4 | 1 | 17,129,219,243,534 |
| <i>Cheirocratus sundevalli</i> | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 105,261,319,484,521 |
| <i>Chlorotocus crassicornis</i> | 3 | 2 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 337 |
| <i>Cidaris cidaris</i> | 3 | 3 | 4 | 2 | 3 | 4 | 3 | 4 | 2 | 337 |
| <i>Colus gracilis</i> | 3 | 1 | 4 | 2 | 3 | 4 | 3 | 3 | 2 | 230,337 |
| <i>Colus islandicus</i> | 3 | 1 | 4 | 2 | 3 | 4 | 3 | 3 | 2 | 230,337 |
| <i>Corbula gibba</i> | 2 | 2 | 3 | 2 | 2 | 2 | 3 | 4 | 1 | 129,247 |
| <i>Corophium</i> sp. | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 180,322,334 |
| <i>Corystes cassivelaunus</i> | 3 | 3 | 3 | 2 | 2 | 3 | 2 | 1 | 1,2 | 179,226,255,319,322 |
| <i>Crangon allmanni</i> | 3 | 2 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 9,44,230 |
| <i>Crangon crangon</i> | 3 | 2 | 3 | 1 | 2 | 3 | 2 | 1 | 1,2 | 108,179,232,397 |
| <i>Diastylis bradyi</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 138,243,264,322,508 |
| <i>Diastylis lucifera</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 102,380,389 |
| <i>Diastylis rathkei</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 389,508 |
| <i>Dichelopandalus bonnieri</i> | 3 | 2 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 230,337 |
| <i>Diogenes pugilator</i> | 2 | 1 | 3 | 2 | 1 | 1 | 2 | 2 | 1 | 309,317,318,490 |
| <i>Donax vittatus</i> | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 4 | 1 | 19,129 |
| <i>Doris pseudoargus</i> | 3 | 2 | 4 | 2 | 1 | 1 | 3 | 3 | 2 | 129,230,486 |
| <i>Dosinia exoleta</i> | 3 | 1 | 2 | 2 | 2 | 4 | 3 | 4 | 1 | 129,190,496,499 |
| <i>Dosinia lupinus</i> | 3 | 1 | 2 | 2 | 2 | 4 | 3 | 3 | 1 | 129,190,497 |
| <i>Dyopedos monacantha</i> | 1 | 2 | 4 | 1 | 1 | 1 | 1 | 2 | 1 | 322,483 |
| <i>Ebalia</i> sp. | 2 | 3 | 4 | 2 | 1 | 2 | 2 | 2 | 1 | 230,295,319,445,446 |
| <i>Ebalia granulosa</i> | 2 | 3 | 4 | 2 | 1 | 2 | 2 | 3 | 2 | 230,295,319,445,446 |
| <i>Ebalia tuberosa</i> | 2 | 3 | 4 | 2 | 1 | 2 | 2 | 3 | 2 | 230,295,319,445,446 |
| <i>Echinocardium</i> sp. | 3 | 3 | 2 | 2 | 3 | 4 | 3 | 3 | 1 | 63,81,243 |
| <i>Echinocardium cordatum</i> | 3 | 3 | 2 | 2 | 3 | 4 | 3 | 3 | 2 | 63,81,243 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|-----------------------------------|----|----|----|----|----|----|----|----|----|-----------------------------|
| <i>Echinocardium pennatifidum</i> | 3 | 3 | 2 | 2 | 3 | 4 | 3 | 3 | 2 | 63,81,243 |
| <i>Echinocyamus pusillus</i> | 2 | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 1 | 198,243,304,319,322 |
| <i>Echinus</i> sp. | 4 | 3 | 4 | 2 | 2 | 4 | 3 | 3 | 2 | 95,151,165,179,183,230,344 |
| <i>Echinus esculentus</i> | 3 | 3 | 4 | 2 | 2 | 4 | 3 | 3 | 2 | 95,151,165,179,183,230,344 |
| <i>Echinus melo</i> | 4 | 3 | 4 | 2 | 2 | 4 | 3 | 3 | 2 | 95,151,165,179,183,230,344 |
| <i>Ensis ensis</i> | 4 | 3 | 2 | 2 | 3 | 4 | 3 | 4 | 1 | 129,233,319 |
| <i>Ensis lei</i> | 4 | 3 | 2 | 2 | 2 | 3 | 3 | 4 | 1 | 129,305,319 |
| <i>Ensis magnus</i> | 4 | 3 | 2 | 2 | 3 | 4 | 3 | 4 | 1 | 115,129,179,236 |
| <i>Ensis siliqua</i> | 4 | 3 | 2 | 2 | 3 | 4 | 3 | 4 | 1 | 116,129,164,233 |
| <i>Eteone flava</i> | 3 | 2 | 3 | 2 | 1 | 1 | 3 | 3 | 1 | 111,230,284,319,376 |
| <i>Eteone longa</i> | 3 | 2 | 3 | 2 | 1 | 1 | 3 | 3 | 1 | 230,243,409,410 |
| <i>Eulalia</i> sp. | 3 | 2 | 4 | 2 | 1 | 3 | 3 | 3 | 1 | 154,190,230,319,322,371 |
| <i>Eumida sanguinea</i> | 2 | 2 | 3 | 2 | 1 | 2 | 3 | 4 | 1 | 65,243,319,322 |
| <i>Eunereis longissima</i> | 4 | 3 | 4 | 2 | 1 | 1 | 3 | 3 | 1 | 190,322,474 |
| <i>Eupolyornia nebulosa</i> | 4 | 3 | 3 | 3 | 2 | 3 | 3 | 3 | 1 | 37,38,211,212,320 |
| <i>Eurydice pulchra</i> | 1 | 2 | 3 | 1 | 2 | 2 | 1 | 1 | 1 | 181,230,262 |
| <i>Eusergestes arcticus</i> | 3 | 2 | 4 | 1 | 2 | 2 | 2 | 1 | 2 | 152,230,327 |
| <i>Euspira catena</i> | 3 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 1 | 18,129,298 |
| <i>Euspira fusca</i> | 3 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 18,129,273,298 |
| <i>Euspira nitida</i> | 2 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 1 | 129,273,298 |
| <i>Fabulina fabula</i> | 2 | 3 | 2 | 2 | 2 | 3 | 3 | 4 | 1 | 129,319,518 |
| <i>Funiculina quadrangularis</i> | 5 | 3 | 4 | 4 | 3 | 4 | 3 | 2 | 2 | 150,210 |
| <i>Galathowenia oculata</i> | 2 | 3 | 3 | 3 | 1 | 1 | 3 | 3 | 1 | 174,274,333 |
| <i>Gammaropsis</i> sp. | 1 | 2 | 4 | 1 | 1 | 2 | 1 | 2 | 1 | 257,319,322,354 |
| <i>Gammarus</i> sp. | 1 | 2 | 4 | 1 | 1 | 2 | 1 | 1 | 1 | 15,103 |
| <i>Gari fervensis</i> | 3 | 1 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 129,131 |
| <i>Gastrosaccus spinifer</i> | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 42,179,313,319,410 |
| <i>Gattyana cirrhosa</i> | 2 | 2 | 1 | 2 | 2 | 3 | 3 | 3 | 1 | 111,243 |
| <i>Gilvossius tyrrenus</i> | 3 | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 148,322,383,480,481 |
| <i>Glycera</i> sp. | 5 | 2 | 1 | 1 | 3 | 3 | 3 | 3 | 1 | 73,106,107,319,322,366,533 |
| <i>Glycymeris glycymeris</i> | 3 | 1 | 3 | 2 | 3 | 4 | 3 | 3 | 2 | 21,189,230,443 |
| <i>Gnathopausia</i> sp. | 3 | 1 | 4 | 1 | 2 | 2 | 1 | 1 | 2 | 335,527 |
| <i>Goneplax rhomboides</i> | 3 | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 230,337 |
| <i>Goniada maculata</i> | 3 | 2 | 3 | 1 | 1 | 2 | 3 | 3 | 1 | 190,243,274,319,320,329 |
| <i>Gracilechinus</i> sp. | 3 | 3 | 4 | 2 | 3 | 4 | 3 | 4 | 2 | 67,187,188,230,308,504,505 |
| <i>Gracilechinus acutus</i> | 3 | 3 | 4 | 2 | 3 | 4 | 3 | 4 | 2 | 188,230,308,505 |
| <i>Gracilechinus elegans</i> | 3 | 3 | 4 | 2 | 3 | 4 | 3 | 4 | 2 | 67,187,188,230,308,504,505 |
| <i>Harmothoe</i> sp. | 3 | 2 | 3 | 2 | 2 | 2 | 2 | 3 | 1 | 111,118,179,243,319,322,410 |
| <i>Harpinia antennaria</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 230,243,322,425,521 |
| <i>Haustorius arenarius</i> | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 137,142,320,506 |
| <i>Hediste diversicolor</i> | 4 | 3 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 144,158,179,322,444 |
| <i>Henricia</i> sp. | 3 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 179,230,337 |
| <i>Heteromastus filiformis</i> | 4 | 3 | 1 | 3 | 2 | 2 | 3 | 3 | 1 | 41,182,453 |
| <i>Hiatella arctica</i> | 3 | 1 | 4 | 4 | 2 | 4 | 3 | 4 | 1 | 129,319,449 |
| <i>Homarus gammarus</i> | 5 | 1 | 1 | 2 | 3 | 4 | 2 | 1 | 2 | 30,246,359,456,513 |
| <i>Hyalinoecia tubicola</i> | 4 | 1 | 4 | 2 | 2 | 2 | 1 | 1 | 2 | 230,337 |
| <i>Hymenodiscus coronata</i> | 5 | 3 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 337 |
| <i>Hypereteone foliosa</i> | 3 | 2 | 2 | 2 | 1 | 2 | 3 | 3 | 1 | 319,322,376,532 |
| <i>Idotea linearis</i> | 2 | 2 | 4 | 1 | 1 | 2 | 1 | 1 | 1 | 179,184,230 |
| <i>Inachus</i> sp. | 3 | 2 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 224,225,294 |
| <i>Inachus dorsettensis</i> | 3 | 2 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 224,225,294 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|--------------------------------|----|----|----|----|----|----|----|----|-----|--|
| <i>Inachus leptochirus</i> | 3 | 2 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 224,225,294 |
| <i>Inachus phalangium</i> | 3 | 2 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 224,225,294 |
| <i>Iphinoe trispinosa</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 101,322,454 |
| <i>Jassa marmorata</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 92,322,429,448 |
| <i>Jorunna tomentosa</i> | 3 | 2 | 4 | 2 | 1 | 1 | 2 | 3 | 2 | 179,230,337 |
| <i>Kellia suborbicularis</i> | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 4 | 1 | 129,300 |
| <i>Kurtiella bidentata</i> | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 1 | 129,230,365 |
| <i>Laetmonice</i> sp. | 2 | 2 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 230,337 |
| <i>Lagis koreni</i> | 3 | 2 | 2 | 3 | 2 | 2 | 3 | 4 | 1 | 125,243,360,482 |
| <i>Lamellaria perspicua</i> | 3 | 2 | 4 | 2 | 1 | 1 | 3 | 3 | 2 | 179,230,337 |
| <i>Lanice conchilega</i> | 4 | 3 | 2 | 3 | 1 | 2 | 3 | 3 | 1 | 179,199,243,278,319,406 |
| <i>Laonice</i> sp. | 4 | 3 | 1 | 3 | 1 | 2 | 3 | 3 | 1 | 47,319,322,458 |
| <i>Lepas</i> sp. | 3 | 1 | 4 | 4 | 1 | 1 | 2 | 3 | 2 | 28,206,230 |
| <i>Lepidonotus squamatus</i> | 3 | 2 | 4 | 2 | 1 | 3 | 3 | 4 | 1 | 322,398,410 |
| <i>Leptometra celtica</i> | 5 | 3 | 4 | 1 | 2 | 2 | 3 | 3 | 2 | 337 |
| <i>Leptosynapta inhaerens</i> | 5 | 3 | 2 | 2 | 2 | 3 | 1 | 1 | 1 | 179,319,322,451 |
| <i>Limecola balthica</i> | 2 | 2 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 129,213,287,307 |
| <i>Liocarcinus</i> sp. | 3 | 1 | 3 | 1 | 2 | 3 | 2 | 1 | 1,2 | 2,25,56,84,85,91,171,179,229,230,319,322 |
| <i>Liocarcinus depurator</i> | 3 | 1 | 3 | 1 | 1 | 3 | 2 | 1 | 2 | 56,171,179,229 |
| <i>Liocarcinus holsatus</i> | 3 | 1 | 4 | 1 | 1 | 3 | 2 | 1 | 2 | 2,84,85,91,230 |
| <i>Liocarcinus marmoreus</i> | 3 | 1 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 2,25,56,84,85,91,171,179,229,230,319,322 |
| <i>Liocarcinus pusillus</i> | 3 | 1 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 2,25,56,84,85,91,171,179,229,230,319,322 |
| <i>Liocarcinus vernalis</i> | 3 | 1 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 2,25,56,84,85,91,171,179,229,230,319,322 |
| <i>Lucinoma borealis</i> | 3 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 1 | 119,129,214,498 |
| <i>Luidia</i> sp. | 5 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 221,230,502 |
| <i>Luidia ciliaris</i> | 5 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 221,230,502 |
| <i>Luidia sarsii</i> | 5 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 221,230,502 |
| <i>Lumbrineris</i> sp. | 5 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 1 | 230,243,319,392,440 |
| <i>Lutaria lutraria</i> | 4 | 1 | 1 | 2 | 3 | 3 | 3 | 4 | 1 | 129,268 |
| <i>Macomangulus tenuis</i> | 2 | 3 | 3 | 2 | 2 | 3 | 3 | 4 | 1 | 20,29,129,133,190,472 |
| <i>Macropipus tuberculatus</i> | 5 | 1 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 216,230,357,367 |
| <i>Macropodia</i> sp. | 3 | 3 | 4 | 2 | 2 | 2 | 2 | 2 | 2 | 179,254,319 |
| <i>Macropodia rostrata</i> | 3 | 3 | 4 | 2 | 2 | 2 | 2 | 2 | 2 | 179,254,319 |
| <i>Macropodia tenuirostris</i> | 3 | 3 | 4 | 2 | 2 | 2 | 2 | 2 | 2 | 179,254,319 |
| <i>Mactra stultorum</i> | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 4 | 1 | 82,129 |
| <i>Magelona filiformis</i> | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 3 | 1 | 175,320,322,347,529 |
| <i>Magelona johnstoni</i> | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 3 | 1 | 175,319,347,529 |
| <i>Magelona mirabilis</i> | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 3 | 1 | 175,347,413,529 |
| <i>Magelona papillicornis</i> | 4 | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 1 | 175,243,322,347,529 |
| <i>Maja brachydactyla</i> | 5 | 1 | 4 | 2 | 2 | 3 | 2 | 1 | 2 | 74,191,217,230 |
| <i>Maja squinado</i> | 5 | 1 | 4 | 2 | 2 | 3 | 2 | 1 | 2 | 217,230,292 |
| <i>Malacoceros fuliginosus</i> | 3 | 3 | 3 | 1 | 2 | 2 | 3 | 3 | 1 | 47,179,215,319 |
| <i>Malmgrenia lunulata</i> | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 4 | 1 | 190,322,395,547 |
| <i>Marthasterias glacialis</i> | 5 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 33,179,230,291,387 |
| <i>Mediomastus fragilis</i> | 3 | 3 | 3 | 3 | 1 | 2 | 3 | 3 | 1 | 190,223,319,410,515 |
| <i>Megaluropus agilis</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 3 | 1 | 161,176,243,382,484 |
| <i>Mesopodopsis slabberi</i> | 2 | 2 | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 136,179,400,520 |
| <i>Mimachlamys</i> sp. | 3 | 2 | 4 | 4 | 2 | 3 | 3 | 4 | 1 | 55,129,412,452 |
| <i>Modiolus</i> sp. | 4 | 1 | 4 | 4 | 3 | 4 | 3 | 4 | 1 | 129,130 |
| <i>Munida intermedia</i> | 4 | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 208,230,296 |
| <i>Munida rugosa</i> | 4 | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 86,208,230,296,394,419,421,435,476 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|-----------------------------------|----|----|----|----|----|----|----|----|-----|---|
| <i>Munida speciosa</i> | 4 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 86,230,394,435 |
| <i>Musculus</i> sp. | 2 | 2 | 4 | 4 | 2 | 3 | 2 | 3 | 1 | 129,310,338 |
| <i>Mya arenaria</i> | 4 | 1 | 1 | 4 | 3 | 4 | 3 | 4 | 1 | 58,59,129 |
| <i>Mya truncata</i> | 3 | 1 | 2 | 4 | 3 | 4 | 3 | 4 | 1 | 11,12,129,319 |
| <i>Mysis undata</i> | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 4 | 1 | 129,190,328 |
| <i>Mytilus</i> sp. | 4 | 1 | 4 | 4 | 2 | 4 | 3 | 4 | 2 | 129,250 |
| <i>Mytilus edulis</i> | 3 | 1 | 4 | 4 | 2 | 4 | 3 | 4 | 1,2 | 129,250 |
| <i>Nassarius reticulatus</i> | 2 | 1 | 3 | 2 | 3 | 3 | 3 | 3 | 1 | 79,129 |
| <i>Natatolana borealis</i> | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 260,265,314,477,484 |
| <i>Nephrops norvegicus</i> | 5 | 1 | 1 | 2 | 3 | 3 | 2 | 1 | 1,2 | 166,168,169,495 |
| <i>Nephtys</i> sp. | 4 | 2 | 2 | 1 | 2 | 3 | 3 | 3 | 1 | 70,93,140,230,243,274,284,319,320,322,326,372,373,374,494,546 |
| <i>Notomastus latericeus</i> | 5 | 3 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 170,200,230,524,528 |
| <i>Nucula nitidosa</i> | 2 | 1 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 125,126,129,413,531 |
| <i>Nucula nucleus</i> | 2 | 1 | 2 | 2 | 2 | 3 | 3 | 3 | 1 | 129,319 |
| <i>Ocenebra erinaceus</i> | 3 | 1 | 4 | 2 | 2 | 2 | 3 | 2 | 2 | 179,324,460,466 |
| <i>Ophelia</i> sp. | 3 | 2 | 3 | 2 | 2 | 2 | 3 | 3 | 1 | 274,319,403 |
| <i>Ophiocomina nigra</i> | 4 | 3 | 4 | 2 | 3 | 4 | 3 | 3 | 2 | 179,230,337 |
| <i>Ophiothrix</i> sp. | 4 | 3 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 127,179,234,469,470 |
| <i>Ophiothrix fragilis</i> | 4 | 3 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 127,179 |
| <i>Ophiothrix luetkeni</i> | 4 | 3 | 4 | 2 | 2 | 2 | 3 | 3 | 2 | 127,179,234,469,470 |
| <i>Ophiura</i> sp. | 3 | 3 | 3 | 1 | 2 | 3 | 3 | 3 | 1,2 | 49,117,179,319,503 |
| <i>Ophiura albida</i> | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 49,117,179,319 |
| <i>Ophiura ophiura</i> | 3 | 3 | 4 | 1 | 2 | 3 | 3 | 3 | 2 | 49,117,179,319,503 |
| <i>Orchomenella nana</i> | 1 | 2 | 4 | 1 | 1 | 1 | 1 | 2 | 1 | 346,484 |
| <i>Owenia fusiformis</i> | 3 | 3 | 2 | 3 | 2 | 2 | 3 | 3 | 1,2 | 13,125,179,196,322,362 |
| <i>Oxydromus flexuosus</i> | 3 | 3 | 3 | 1 | 2 | 2 | 3 | 3 | 1 | 220,381 |
| <i>Pagurus</i> sp. | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus alatus</i> | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus bernhardus</i> | 3 | 1 | 4 | 2 | 2 | 3 | 2 | 1 | 1,2 | 128,179,288,321 |
| <i>Pagurus carneus</i> | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus cuanensis</i> | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus excavatus</i> | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus forbesii</i> | 2 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Pagurus prideaux</i> | 3 | 2 | 4 | 2 | 2 | 2 | 2 | 1 | 2 | 128,179,275,276,288,321 |
| <i>Palaemon serratus</i> | 3 | 2 | 4 | 1 | 1 | 2 | 2 | 1 | 2 | 178,179,230,414 |
| <i>Palinurus elephas</i> | 5 | 1 | 1 | 1 | 3 | 4 | 2 | 1 | 2 | 207,242 |
| <i>Palinurus mauritanicus</i> | 5 | 1 | 1 | 1 | 3 | 4 | 2 | 1 | 2 | 207,242 |
| <i>Paraonis fulgens</i> | 3 | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 1 | 157,319,410,418,536 |
| <i>Parapenaeus longirostris</i> | 3 | 1 | 4 | 1 | 2 | 2 | 3 | 2 | 2 | 241,272,461 |
| <i>Parastichopus regalis</i> | 5 | 1 | 4 | 2 | 3 | 3 | 3 | 3 | 2 | 337 |
| <i>Parastichopus tremulus</i> | 4 | 1 | 4 | 2 | 3 | 3 | 3 | 3 | 2 | 337 |
| <i>Paromola cuvieri</i> | 5 | 1 | 4 | 2 | 2 | 3 | 2 | 1 | 2 | 337 |
| <i>Pasiphaea multidentata</i> | 3 | 2 | 4 | 1 | 2 | 2 | 2 | 1 | 2 | 22,72,96,152,230,327 |
| <i>Pasiphaea sivado</i> | 3 | 2 | 4 | 1 | 2 | 2 | 2 | 1 | 2 | 72,96,230,327,526 |
| <i>Pasiphaea tarda</i> | 3 | 2 | 4 | 1 | 2 | 2 | 2 | 1 | 2 | 22,152,230,327 |
| <i>Pecten maximus</i> | 4 | 1 | 4 | 1 | 2 | 4 | 3 | 4 | 2 | 129 |
| <i>Pennatula phosphorea</i> | 4 | 2 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 230,337 |
| <i>Peringia ulvae</i> | 1 | 2 | 3 | 2 | 1 | 2 | 3 | 3 | 1 | 14,129,179,462 |
| <i>Periculodes longimanus</i> | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 31,243,484 |
| <i>Petricolaria pholadiformis</i> | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 4 | 1 | 8,129,147,426 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|--------------------------------|----|----|----|----|----|----|----|----|-----|--|
| <i>Phaxas pellucidus</i> | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 3 | 1 | 129,299 |
| <i>Philine aperta</i> | 3 | 2 | 4 | 2 | 2 | 2 | 3 | 4 | 2 | 179,245 |
| <i>Philocheras echinulatus</i> | 2 | 2 | 3 | 1 | 1 | 1 | 2 | 1 | 2 | 230,283,368,369,391 |
| <i>Philocheras trispinosus</i> | 2 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 230,283,368,369,391 |
| <i>Pholoe minuta</i> | 1 | 2 | 3 | 2 | 3 | 3 | 3 | 3 | 1 | 87,231,322 |
| <i>Phoronis</i> sp. | 3 | 3 | 2 | 3 | 1 | 1 | 3 | 4 | 1 | 153 |
| <i>Photis longicaudata</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 3 | 1 | 261,345,353,484,525 |
| <i>Phyllodoce</i> sp. | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 1 | 230,243,302,349 |
| <i>Pisidia longicornis</i> | 1 | 3 | 4 | 2 | 1 | 2 | 3 | 3 | 2 | 230,431,459 |
| <i>Pisione remota</i> | 3 | 2 | 3 | 2 | 2 | 2 | 3 | 4 | 1 | 146,319,320,471 |
| <i>Plesionika heterocarpus</i> | 3 | 2 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 6,7,94,97,192,241,289,315,377,379,408,434,46 |
| <i>Plesionika martia</i> | 3 | 2 | 4 | 1 | 2 | 2 | 2 | 1 | 2 | 241,315 |
| <i>Poecilochaetus serpens</i> | 3 | 3 | 3 | 3 | 1 | 1 | 3 | 3 | 1 | 132,170,190,319,322 |
| <i>Polybius henslowii</i> | 2 | 2 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Polycheles typhlops</i> | 3 | 1 | 1 | 1 | 3 | 3 | 2 | 1 | 2 | 1,5,98,242,492 |
| <i>Polydora</i> sp. | 2 | 3 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 16,90,120,179,215,311,322,545 |
| <i>Pontocrates altamarinus</i> | 1 | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 31,243 |
| <i>Pontocrates arcticus</i> | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 31,32,320 |
| <i>Pontocrates arenarius</i> | 1 | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 31,176,320,514 |
| <i>Pontophilus norvegicus</i> | 3 | 2 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Pontophilus spinosus</i> | 3 | 2 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Porania pulvillus</i> | 4 | 1 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 230,337 |
| <i>Portumnus latipes</i> | 3 | 3 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 100,230,301,501 |
| <i>Prionospio</i> sp. | 3 | 2 | 3 | 3 | 1 | 1 | 3 | 3 | 1 | 319,322,363 |
| <i>Processa</i> sp. | 2 | 2 | 3 | 1 | 1 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Processa canaliculata</i> | 2 | 2 | 3 | 1 | 1 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Processa nouveli</i> | 2 | 2 | 3 | 1 | 1 | 2 | 2 | 1 | 2 | 230,337 |
| <i>Psammechinus miliaris</i> | 3 | 3 | 4 | 2 | 2 | 3 | 3 | 4 | 1,2 | 50,179,230,267 |
| <i>Pseudocuma longicorne</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 101,319,322,454 |
| <i>Pteria hirundo</i> | 4 | 1 | 4 | 4 | 3 | 4 | 3 | 4 | 2 | 197,340,341,441,442,464,516 |
| <i>Pteroeides griseum</i> | 5 | 2 | 4 | 4 | 3 | 4 | 3 | 3 | 2 | 337 |
| <i>Pycnogonum litorale</i> | 2 | 1 | 4 | 2 | 2 | 3 | 1 | 3 | 2 | 23,179,256,491 |
| <i>Pygospio elegans</i> | 2 | 3 | 3 | 3 | 1 | 2 | 2 | 3 | 1 | 16,320 |
| <i>Rissoides desmaresti</i> | 3 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 235,242,511 |
| <i>Rostanga rubra</i> | 2 | 2 | 4 | 2 | 1 | 1 | 3 | 4 | 2 | 83,204,205,230 |
| <i>Scalibregma inflatum</i> | 3 | 2 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 45,143,170,312 |
| <i>Scaphander lignarius</i> | 3 | 2 | 4 | 2 | 2 | 2 | 3 | 4 | 2 | 230,337 |
| <i>Schistomysis</i> sp. | 2 | 2 | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 230,319,330,400,432,433 |
| <i>Scolecopsis squamata</i> | 3 | 3 | 1 | 1 | 2 | 2 | 3 | 3 | 1 | 47,121,243,465,473 |
| <i>Scoletoma fragilis</i> | 5 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 1 | 230,376,507 |
| <i>Scoloplos armiger</i> | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 1 | 77,201,243,279,447 |
| <i>Sergia robusta</i> | 3 | 2 | 4 | 1 | 2 | 3 | 2 | 1 | 2 | 337 |
| <i>Sigalion mathildae</i> | 3 | 2 | 1 | 2 | 3 | 3 | 3 | 3 | 1 | 179,199,243,333 |
| <i>Solenocera membranacea</i> | 3 | 2 | 3 | 2 | 1 | 1 | 2 | 2 | 2 | 337 |
| <i>Spatangus purpureus</i> | 4 | 3 | 3 | 2 | 3 | 3 | 3 | 4 | 2 | 179,230,337 |
| <i>Sphenia binghami</i> | 2 | 3 | 4 | 4 | 3 | 4 | 3 | 4 | 1 | 129,222,319,540 |
| <i>Spio decoratus</i> | 2 | 3 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 123,199,218,230 |
| <i>Spio filicornis</i> | 2 | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 243,467,475 |
| <i>Spio martinensis</i> | 2 | 3 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 123,215,230,319,475 |
| <i>Spiophanes bombyx</i> | 3 | 3 | 3 | 3 | 1 | 2 | 3 | 3 | 1 | 47,113,243,413 |
| <i>Spirobranchus triqueter</i> | 2 | 1 | 4 | 3 | 1 | 2 | 3 | 4 | 1 | 104,179,281 |

Table S1.1. Continued.

| Taxon | BL | FR | BD | MO | AM | LS | OT | OS | CS | References |
|-------------------------------|----|----|----|----|----|----|----|----|-----|-----------------------|
| <i>Spisula elliptica</i> | 2 | 1 | 3 | 2 | 2 | 3 | 3 | 4 | 1 | 129,190,319 |
| <i>Spisula solida</i> | 3 | 1 | 3 | 2 | 3 | 4 | 3 | 4 | 1 | 129,163,179,259 |
| <i>Spisula subtruncata</i> | 2 | 1 | 3 | 2 | 2 | 3 | 3 | 4 | 1 | 68,125,129 |
| <i>Stichastrella rosea</i> | 3 | 2 | 4 | 2 | 2 | 3 | 3 | 3 | 2 | 230,337 |
| <i>Streblospio shrubsolii</i> | 2 | 2 | 3 | 3 | 1 | 1 | 1 | 2 | 1 | 76,230,277,436 |
| <i>Streptosyllis websteri</i> | 1 | 2 | 3 | 2 | 3 | 3 | 3 | 3 | 1 | 194,230,333 |
| <i>Synchelidium maculatum</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 31,484,514,543 |
| <i>Tellimya ferruginosa</i> | 1 | 3 | 2 | 2 | 1 | 2 | 2 | 4 | 1 | 129,230,300,370 |
| <i>Terebellides stroemii</i> | 2 | 3 | 2 | 3 | 1 | 2 | 3 | 3 | 1 | 111,145,170,384 |
| <i>Tethyaster subinermis</i> | 5 | 2 | 4 | 2 | 3 | 4 | 3 | 3 | 2 | 337 |
| <i>Tharyx</i> sp. | 2 | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 1 | 48,125,167,203,393 |
| <i>Thelepus cincinnatus</i> | 4 | 2 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 190,258,332 |
| <i>Thracia convexa</i> | 3 | 3 | 2 | 2 | 2 | 3 | 2 | 3 | 1 | 10,80,129,319,437 |
| <i>Thracia phaseolina</i> | 2 | 3 | 1 | 2 | 2 | 4 | 2 | 3 | 1 | 10,129,319,437 |
| <i>Thracia pubescens</i> | 3 | 3 | 2 | 2 | 2 | 4 | 2 | 3 | 1 | 10,129,319,364,437 |
| <i>Thyasira flexuosa</i> | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 1 | 43,125,129,306 |
| <i>Turritella communis</i> | 3 | 1 | 3 | 2 | 2 | 3 | 3 | 4 | 1,2 | 129,297,322 |
| <i>Upogebia deltaura</i> | 3 | 3 | 1 | 2 | 2 | 3 | 2 | 1 | 1 | 319,322,500,519 |
| <i>Urothoe brevicornis</i> | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 65,99,132,243,319 |
| <i>Urothoe marina</i> | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 65,99,132,179,319 |
| <i>Urothoe poseidonis</i> | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 65,99,132,179,243,319 |
| <i>Venerupis corrugata</i> | 3 | 1 | 2 | 4 | 2 | 3 | 3 | 4 | 1 | 129 |
| <i>Venus</i> sp. | 3 | 1 | 3 | 2 | 3 | 4 | 3 | 4 | 1 | 24,129,178,399 |
| <i>Venus casina</i> | 2 | 1 | 3 | 2 | 2 | 3 | 3 | 4 | 2 | 24,129,178,399 |
| <i>Westwoodilla caecula</i> | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 32,320 |
| <i>Xylophaga dorsalis</i> | 2 | 1 | 3 | 3 | 1 | 1 | 3 | 4 | 2 | 109,110,195,422 |

REFERENCES

- Abelló P., Cartes J.E., 1992. Population characteristics of the deep-sea lobsters *Polychaetes typhlops* and *Stereomastis sculpata* (Decapoda: Polychelidae) in a bathyal mud community of the Mediterranean Sea. *Marine Biology* 114:109–117.
- Abelló P., Reid D.G., Naylor E., 1991. Comparative locomotor activity patterns in the portunid crabs *Liocarcinus holsatus* and *L. depurator*. *Journal of the Marine Biological Association of the United Kingdom* 71:1–10.
- Abrams P.A., Hill C., Elmgren R., 1990. The functional response of the predatory polychaete, *Harmothoe sarsi*, to the amphipod, *Pontoporeia affinis*. *Oikos* 59:261–269.
- Adkins M., Schulze A., 2011. Development of *Capitella* sp. G from Galveston Bay, Texas. *Marine Biology Research* 7:202–207.
- Aguzzi J., Bahamon N., 2009. Modeled day–night biases in decapod assessment by bottom trawling survey. *Fisheries Research* 100:274–280.
- Ahamed F., Ohtomi J., 2011. Reproductive biology of the pandalid shrimp *Plesionika izumiae* (Decapoda: Caridea). *Journal of Crustacean Biology* 31:441–449.
- Ahamed F., Ohtomi J., 2012. Growth patterns and longevity of the pandalid shrimp *Plesionika izumiae* (Decapoda: Caridea). *Journal of Crustacean Biology* 32:733–740.
- Alexander R.R., Stanton R.J. Jr., Dodd J.R., 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.
- Allen J.A., 1960. On the biology of *Crangon allmani* Kinahan in Northumberland Waters. *Journal of the Marine Biological Association of the United Kingdom* 39:481–508.
- Allen J.A., 1961. The British species of *Thracia* (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom* 41:723–735.
- 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)? *Helgolander Marine Research* 57:132–138.
- Amaro T., Duineveld G., Tyler P., 2005. Does *Mya truncata* reproduce at its southern distribution limit? *Journal of Shellfish Research* 24:25–28.
- Ambrogi R., Fontana P., Gambi M.C., 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 A., 1971. Intertidal activity, breeding and the floating habit of *Hydrobia ulvae* in the Ythan estuary. *Journal of the Marine Biological Association of the United Kingdom* 51:23–37.

15. Andersson S., Persson M., Moksnes P.O., Baden S., 2009. The role of the amphipod *Gammarus locusta* as a grazer on macroalgae in Swedish seagrass meadows. *Marine Biology* 156:969–981.
16. Anger K., Anger V., Hagmeier E., 1986. Laboratory studies on larval growth of *Polydora ligni*, *Polydora ciliata*, and *Pygospio elegans* (Polychaeta, Spionidae). *Helgoländer Meeresuntersuchungen* 40:377–395.
17. Ansell A.D., 1961. Reproduction, growth and mortality of *Venus striatula* (Da Costa) in Kames Bay, Millport. *Journal of the Marine Biological Association of the United Kingdom* 41:191–215.
18. Ansell A.D., 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 A.D., 1983. The biology of the genus *Donax*. *Developments in Hydrobiology* 19:607–635.
20. Ansell A.D., Trevallion A., 1967. Studies on *Tellina tenuis* da costa I. Seasonal growth and biochemical cycle. *Journal of Experimental Marine Biology and Ecology* 1:220–235.
21. Ansell A.D., Trueman E.R., 1967. Observations on burrowing in *Glycymeris glycymeris* (L.) (Bivalvia, Arcacea). *Journal of Marine Experimental Biology and Ecology* 1:65–75.
22. Apollonio S., 1969. Breeding and fecundity of the glass shrimp, *Pasiphaea multidentata* (Decapoda, Caridea), in the Gulf of Maine. *Journal of the Fisheries Research Board of Canada* 26:1969–1983.
23. Arnaud F., Bamber R.N., 1988. The biology of Pycnogonida. *Advances in Marine Biology* 24:1–96.
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. *Fisheries Research* 38:193–198.
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.
26. Barbaglio A., Turchi C., Melone G., Di Benedetto C., Martinello T., Patruno M., Biggiogero M., Wilkie I.C., Candia Carnevali M.D., 2012. Offspring development in the feather star *Antedon mediterranea*. *Invertebrate Reproduction and Development* 56:124–137.
27. Barnes H., Barnes M., 1954. The general biology of *Balanus balanus* (L.) Da Costa. *Oikos* 5:63–76.
28. Barnes M., 1996. Pedunculate cirripedes of the genus *Pollicipes*. *Oceanography and Marine Biology – An Annual Review* 34:303–394.
29. Barnett P.R.O., 1985. The effect of temperature on the growth of planktonic larvae of *Tellina tenuis* da Costa. *Journal of Experimental Marine Biology and Ecology* 89:1–10.
30. Beard T.W., McGregor D., 2004. Storage and care of live lobsters. *Laboratory Leaflet Number 66 (Revised)*. Lowestoft, Centre for Environment, Fisheries and Aquaculture Science, 28 p.
31. Beare D.J., Moore P.G., 1998. Aspects of the life histories of *Perioculodes longimanus*, *Pontocrates arcticus* and *Synchelidium maculatum* (Crustacea: Amphipoda) at Millport, Scotland. *Journal of the Marine Biological Association of the United Kingdom* 78:193–209.
32. Beare D.J., Moore P.G., 1998. The life histories of offshore oedicerotids *Weswoodilla caecula* and *Monoculodes packardii* (Crustacea: Amphipoda) from Loch Fyne, Scotland. *Journal of the Marine Biological Association of the United Kingdom* 78:835–852.
33. Benitez Villalobos F., 2005. Reproduction and larval biology of North Atlantic asteroids related to the invasion of the Deep sea. PhD thesis, University of Southampton, 138 p.
34. Bennett D.B., 1974. Growth of the edible crab (*Cancer pagurus* L.) off south-west England. *Journal of the Marine Biological Association of the United Kingdom* 54:803–823.
35. Berrill M., 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *Journal of Crustacean Biology* 2:31–39.
36. Bertrand S., Escriva H., 2011. Evolutionary crossroads in developmental biology: Amphioxus. *Development* 138:4819–4830.
37. 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.
38. Bhaud M.R., 1991. Larval release from the egg mass and settlement of *Eupolyornia nebulosa* (Polychaeta, Terebellidae). *Bulletin of Marine Science* 48:420–431.
39. Bigford T.E., 1979. Synopsis of biological data on the Rock Crab, *Cancer irroratus* Say. NOAA Technical Report NMFS Circular 426, FAO Synopsis No. 123, National Marine Fisheries Service, 26 p.
40. Bigot J.L., 1979. Identification des zoés de tourteau (*Cancer pagurus* L.) et d'étrille (*Macropipus puber* L.). Comparaison avec d'autres zoés de morphologie très voisine. *Conseil International pour l'Exploration de la Mer, Comité de l'Océanographie biologique, C.M. 1979/L :17*.
41. Bijkerk R., Dekker P.I., 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.
42. Biju A., 2008. Studies on taxonomy and ecology of Mysidacea from the EEZ of India. PhD thesis, National Institute of Oceanography, Cochin, India, 1962 p.
43. Blacknell W.N., 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.
44. Blahudka S., Türkay M., 2002. A population study of the shrimp *Crangon allmanni* in the German Bight. *Helgolander Marine Research* 56:190–197.
45. Blake J.A., 1993. Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom* 73:123–141.
46. Blake J.A., 2009. Redescription of *Capitella capitata* (Fabricius) from West Greenland and designation of a neotype (Polychaeta, Capitellidae). *Zoosymposia* 2:55–80.

47. Blake J.A., Arnofsky P.L., 1999. Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia* 402:57–106.
48. Blake J.A., 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.
49. Boos K., Gutov L., Mundry R., Franke H.D., 2010. Sediment preference and burrowing behaviour in the sympatric brittlestars *Ophiura albida* Forbes, 1839 and *Ophiura ophiura* (Linnaeus, 1758) (Ophiuroidea, Echinodermata). *Journal of Experimental Marine Biology and Ecology* 393:176–181.
50. Borei H., 1948. Respiration of oocytes, unfertilized eggs and fertilized eggs from *Psammechinus* and *Asterias*. *The Biological Bulletin* 95:1124–150.
51. Bos O.G., Witbaard R., Lavaleye M., van Moorsel G., Teal L.R., van Hal R., van der Hammen T., ter Hofstede R., van Bemmelen R., Witte R.H., Geelhoed S., Dijkman E.M., 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.
52. Bourgoin A., Guillou M., 1988. Démographie d'*Amphiura filiformis* (Echinodermata : Ophiuroidea) en baie de Concarneau (Finistère, France). *Oceanologica Acta* 11:79–87.
53. Bourgoin A., Guillou M., 1990. Variations in the reproductive cycle of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) according to environment in the Bay of Douarnenez (Brittany). *Journal of the Marine Biological Association of the United Kingdom* 70:57–66.
54. Bourgoin A., Guillou M., 1994. Arm regeneration in two populations of *Acrocnida brachiata* (Montagu) (Echinodermata: Ophiuroidea) in Douarnenez Bay, (Brittany: France): an ecological significance. *Journal of Experimental Marine Biology and Ecology* 184:123–139.
55. Brand A.R., 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. Bridges C.R., 1986. A comparative study of the respiratory properties and physiological function of haemocyanin in two burrowing and two non-burrowing crustaceans. *Comparative Biochemistry and Physiology Part A: Physiology* 83:261–270.
57. Broom M.J., 1976. Synopsis on biological data on scallops. Food and Agriculture Organisation of the United Nations. FAO Fisheries Synopsis No. 114, 44 p.
58. Brousseau D.J., 1978. Spawning cycle, fecundity, and recruitment in a population of soft-shell clam, *Mya arenaria*, from Cape Ann, Massachusetts. *Fishery Bulletin* 76:155–166.
59. Brousseau D.J., 1979. Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Marine Biology* 51:221–227.
60. Brown R.A., 1982. Reproduction of *Abra nitida* (Müller) (Bivalvia) in the southern Skagerrak. *Sarsia* 67:55–60.
61. Buchanan J.B., 1963. The biology of *Calocaris macandreae* (Crustacea: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom* 43:729–747.
62. Buchanan J.B., 1964. A comparative study of some features of the biology of *Amphiura filiformis* and *Amphiura chiajei* (Ophiuroidea) considered in relation to their distribution. *Journal of the Marine Biological Association of the United Kingdom* 44:565–576.
63. Buchanan J.B., 1966. The biology of *Echinocardium cordatum* (Echinodermata: Spatangoidea) from different habitats. *Journal of the Marine Biological Association of the United Kingdom* 46:97–114.
64. Buchanan J.B., 1967. Dispersion and demography of some infaunal echinoderm populations. *Symposia of the Zoological Society of London* 20:1–11.
65. Callaway R., 2006. Tube worms promote community change. *Marine Ecology Progress Series* 308:49–60.
66. Campbell G., Russell M., 2014. Direct evidence for bottom-fishing in archaeological whelks (*Buccinum undatum*). In: Fernandes R., Meadows J. (editors). *Human Exploitation of Aquatic Landscapes*. Special issue, *Internet Archaeology* doi:10.11141/ia.37.6.
67. Campos-Creaset L.S., Tyler P.A., Gage J.D., John W.G., 1994. Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis*. *Deep-Sea Research I* 41:369–388.
68. Cardoso J.F.M.F., Witte J.I.J., van der Veer H.W., 2007. Growth and reproduction of the bivalve *Spisula subtruncata* (da Costa) in Dutch coastal waters. *Journal of Sea Research* 57:316–324.
69. Cargnelli L.M., Griesbach S.J., Packer D.B., 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.
70. 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. *Marine Biology* 124:537–550.
71. Carroll J.C., Winn R.N., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) – Brown Rock Crab, Red Rock Crab, and Yellow Crab. U.S. Fish and Wildlife Service, Biological Report 82 (11.117), U.S. Army Corps of Engineers, TR EL-82-4, 16 p.
72. Cartes J.E., 1993. Feeding habits of pasiphaeid shrimps close to the bottom on the Western Mediterranean slope. *Marine Biology* 117:459–468.
73. Casaux C., 1967. Développement larvaire de *Glycera convulata* Keferstein. *Vie et Milieu* 18:559–572.
74. Castejón D., Rotllant G., Giménez L., Torres G., Guerao G., 2015. The Effects of temperature and salinity on the survival, growth and duration of the offspring development of the common spider crab *Maja brachydactyla* (Balss, 1922) (Brachyura: Majidae). *Journal of Shellfish Research* 34:1073–1083.
75. Cazaux C., 1968. Etude morphologique du développement larvaire d'annélides polychètes (Bassin d'Arcachon). 1. Aphroditidae, Chrysopetalidae. *Archives de zoologie expérimentale et générale* 109:477–543.
76. Cazaux C., 1985. Reproduction et développement larvaire de l'annélide polychète saumâtre *Streblospio shrubsolii*. *Cahiers de Biologie Marine* 26:207–221.

77. Chapman G., 1965. The egg cocoons of *Scoloplos armiger* O. F. Müller. *Biological Bulletin* 128:189–197.
78. Chatterton T.D., 1990. Aspects of the population biology and ecology of the New Zealand cancer crab, *Cancer novaezelandiae* (Jacquinot, 1853). PhD thesis, University of Otago, 190 p.
79. Chatzinikolaou E., Richardson C.A., 2010. Parental size and environmental conditions affect egg capsule production by *Nassarius reticulatus* (Linnaeus 1758) (Gastropoda: Nassariidae). *Journal of Experimental Marine Biology and Ecology* 390:14–21.
80. Checa A., Harper E.M., Willinger M., 2012. Aragonitic dendritic prismatic shell microstructure in *Thracia* (Bivalvia, Anomalodesmata). *Invertebrate Biology* 131:19–29.
81. Chen P.S., 1958. Further studies on free amino-acids and peptides in eggs and embryos of different sea-urchin species and hybrids. *Experientia* 14:369–371.
82. Chetoui I., Telahigue K., Bejaoui S., Rabeh I., Ghribi F., Denis F., El Cafsi M., 2019. Annual reproductive cycle and condition index of *Maetra corallina* (Mollusca: Bivalvia) from the north coast of Tunisia. *Invertebrate Reproduction & Development* 63:40–50.
83. Chia F.S., Koss R., 1978. Development and metamorphosis of the planktotrophic larvae of *Rostanga pulchra* (Mollusca: Nudibranchia). *Marine Biology* 46:109–119.
84. Choy S., 1988. Reproductive Biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. *Marine Ecology* 9:227–241.
85. Choy S.C., 1991. Embryonic and larval biology of *Liocarcinus holsatus* and *Necora puber* (Crustacea: brachyura: portunidae). *Journal of Experimental Marine Biology and Ecology* 148:77–92.
86. Christiansen M.E., Anger K., 1990. Complete larval development of *Galathea intermedia* Lilljeborg reared in laboratory culture (Anomura: Galatheididae). *Journal of Crustacean Biology* 10:87–111.
87. Christie G., 1982. The reproductive cycles of two species of *Pholoe* (Polychaeta: Sigalionidae) off the Northumberland coast. *Sarsia* 67:283–292.
88. Christie G., 1985. A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *Journal of the Marine Biological Association of the United Kingdom* 65:239–254.
89. Chung J.S., Chung E.Y., Lee C.H., 2012. Gametogenic cycle and the number of spawning seasons by quantitative statistical analysis, and the size at 50 % of group sexual maturity in *Atrina* (*Servatrina*) *pectinata* (Bivalvia: Pinnidae) in Western Korea. *Korean Journal of Malacology* 28:363–375.
90. Çinar M.E., Ergen Z., Dagli E., Petersen M.E., 2005. Alien species of spionid polychaetes (*Streblospio gynobranchiata* and *Polydora cornuta*) in Izmir Bay, eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* 85:821–827.
91. Clark P.F., 1984. A comparative study of zoeal morphology in the genus *Liocarcinus* (Crustacea: Brachyura: Portunidae). *Zoological Journal of the Linnean Society* 82:273–290.
92. Clark R., Caudill C.C., 2001. Females of the marine amphipod *Jassa marmorata* mate multiple times with the same or different males. *Marine and Freshwater Behaviour and Physiology* 34:131–138.
93. Clark R.B., 1962. Observations on the food of *Nephtys*. *Limnology and Oceanography* 7:380–385.
94. Colloca F., 2009. Life cycle of the deep-water pandalid shrimp *Plesionika edwardsii* (Decapoda, Caridea) in the central Mediterranean Sea. *Journal of Crustacean Biology* 22:775–783.
95. Comely C.A., Ansell A.D., 1989. The reproductive cycle of *Echinus esculentus* L. on the Scottish West Coast. *Estuarine, Coastal and Shelf Science* 29:385–407.
96. Company J.B., Cartes J.E., Sardà F., 2001. Biological patterns and near-bottom population characteristics of two pasiphaeid decapod crustacean species, *Pasiphaea sivado* and *P. multidentata*, in the north-western Mediterranean Sea. *Marine Biology* 139:61–73.
97. Company J.B., Sardà F., 1997. Reproductive patterns and population characteristics in five deep-water pandalid shrimps in the Western Mediterranean along a depth gradient (150–1100 m). *Marine Ecology Progress Series* 148:49–58.
98. Company J.B., Sardà F., 2000. Growth parameters of deep-water decapod crustaceans in the northwestern Mediterranean Sea: a comparative approach. *Marine Biology* 136:79–90.
99. Conradi M., López-González P.J., Bellan-Santini D., 1995. A new species of *Urothoe* (Amphipoda, Gammaridea) from the Iberian peninsula. *Cahiers de Biologie Marine* 36:9–13.
100. Cores Reyes C., 2015. Biology, ecology and dynamics of Pennant's swimming crab (*Portunus latipes*) in the South of Portugal. MSc thesis, University of Algarve, 111 p.
101. Corey S., 1969. The comparative life histories of three Cumacea (Crustacea): *Cumopsis goodsiri* (Van Beneden), *Iphinoe trispinosa* (Goodsir), and *Pseudocuma longicornis* (Bate). *Canadian Journal of Zoology* 47:695–704.
102. Corey S., 1981. Comparative fecundity and reproductive strategies in seventeen species of the Cumacea (Crustacea: Peracarida). *Marine Biology* 62:65–72.
103. Costa F.O., Costa M.H., 1999. Life history of the amphipod *Gammarus locusta* in the Sado estuary (Portugal). *Acta Oecologica* 20:305–314.
104. Cotter E., O'Riordan R.M., Myers A.A., 2003. A histological study of reproduction in the serpulids *Pomatoceros triquetus* and *Pomatoceros lamarckii* (Annelida: Polychaeta). *Marine Biology* 142:905–914.
105. Crawford G.I., 1937. Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 21:631–643.
106. Creaser E.P. Jr., 1973. Reproduction of the bloodworm (*Glycera dibranchiata*) in the Sheepscot Estuary, Maine. *Journal of the Fisheries Research Board of Canada* 30:161–166.
107. Creaser E.P. Jr., Clifford D.A., Hogan M.J., Sampson D.B., 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.

108. Criales M.M., Anger K., 1986. Experimental studies on the offspring development of the shrimps *Crangon crangon* and *C. Allmanni*. *Helgoländer Meeresuntersuchungen* 40:241–265.
109. Culliney I.L., Turner R.D., 1976. Larval development of the deep-water wood boring bivalve, *Xylophaga atlantica* Richards (Mollusca, Bivalvia, Pholadidae). *Ophelia* 15:149–161.
110. Cunningham Miller R., 1924. The boring habits of the shipworm. *The Scientific Monthly* 19:433–440.
111. Curtis M.A., 1977. Life cycles and population dynamics of marine benthic polychaetes from the Disko bay area of West Greenland. *Ophelia* 16:9–58.
112. D'Onghia G., Maiorano P., Matarrese A., Tursi A., 1998. Distribution, biology, and population dynamics of *Aristaeomorpha foliacea* (Risso, 1827) (Decapoda, Natantia, Aristeidae) in the north-western Ionian Sea (Mediterranean Sea). *Crustaceana* 71:518–544.
113. D'Andrea A.F., Lopez G.R., Aller R.C., 2004. Rapid physical and biological particle mixing on an intertidal sandflat. *Journal of Marine Research* 62:67–92.
114. d'Udekem d'Acoz C., 2004. The genus *Bathyporeia* Lindström, 1855, in western Europe (Crustacea: Amphipoda: Pontoporeiidae). *Zoologische Verhandlungen* 348:3–162.
115. da Costa F., Darriba S., Martínez-Patiño D., 2006. Embryonic and offspring development of *Ensis arcuatus* (Jeffreys, 1865) (Bivalvia: Pharidae). *Journal of Molluscan Studies* 74:103–109.
116. da Costa F.D., Martínez-Patiño D., Ojea J., Nóvoa S., 2010. Larval rearing and spat production of the razor clam *Ensis siliqua* (Bivalvia: Pharidae). *Journal of Shellfish Research* 29:347–351.
117. Dahm C., 1993. Growth, production and ecological significance of *Ophiura albida* and *O. ophiura* (Echinodermata: Ophiuroidea) in the German Bight. *Marine Biology* 116:431–437.
118. Daly J.M., 1972. The maturation and breeding biology of *Harmothoe imbricata* (Polychaeta: Polynoidae). *Marine Biology* 12:53–66.
119. Dando P.R., Southward A.J., Southward E.C., 1986. Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proceedings of the Royal Society B: Biological Sciences* 227:227–247.
120. Daro M.H., Polk P., 1973. The autecology of *Polydora ciliata* along the Belgian coast. *Netherlands Journal of Sea Research* 6:130–140.
121. Dauer D.M., 1983. Functional morphology and feeding behavior of *Scolecopsis squamata* (Polychaeta: Spionidae). *Marine Biology* 77:279–285.
122. Dauvin J.C., 1988. Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 2. *Ampelisca brevicornis* (Costa). *Journal of Experimental Marine Biology and Ecology* 119:213–233.
123. Dauvin J.C., 1989. Sur la présence de *Spio decoratus* Bobretzky, 1871 en Manche et remarques sur *Spio martinensis* Mesnil, 1896 et *Spio filicomis* (O.F. Müller, 1776). *Cahiers de Biologie Marine* 30:167–180.
124. Dauvin J.C., Gentil F., 1989. Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (Western English Channel). *Marine Biology* 103:63–73.
125. Dauwe B., Herman P.M.J., Heip C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Marine Ecology Progress Series* 173:67–83.
126. Davis J.P., Wilson J.G., 1983. The population structure and ecology of *Nucula turgida* (Leckenby & Marshall) in Dublin Bay. *Progress in Underwater Science* 8:53–60.
127. Davoult D., Gounin F., Richard A., 1990. Dynamique et reproduction de la population d'*Ophiolithrix fragilis* (Abildgaard) du détroit du Pas-de-Calais (Manche orientale). *Journal of Experimental Marine Biology and Ecology* 138:201–216.
128. Dawirs R.R., 1979. Effects of temperature and salinity on larval development of *Pagurus bernhardus* (Decapoda, Paguridae). *Marine Ecology Progress Series* 1:323–329.
129. de Bruyne R., van Leeuwen S., Gmelig Meyling A., Daan R., 2013. *Schelpdieren van het Nederlandse Noordzeegebied*. Tirion Uitgevers, Utrecht, Nederland, 414 p.
130. de Schweinitz E.H., Lutz R.A., 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. *The Biological Bulletin* 150:348–360.
131. Deart Y.V., Frolov A.A., Manushin I.E., 2013. Bivalves *Abra prismatica* (Montagu, 1808) and *Gari fervensis* (Gmelin, 1791)—Species new to the fauna of the Russian sector of the Barents Sea. *Russian Journal of Biological Invasions* 4:139–148.
132. Degraer S., Wittoeck J., Appeltans W., Cooreman K., Deprez T., Hillewaert H., Hostens K., Mees J., Van den Berghe W., Vincx M., 2006. The macrobenthos atlas of the Belgian part of the North Sea. University of Gent, 164 p.
133. 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. *Journal of Sea Research* 42:207–220.
134. Dekker R., Beukema J.J., 1993. Dynamics and growth of a bivalve, *Abra tenuis*, at the northern edge of its distribution. *Journal of the Marine Biological Association of the United Kingdom* 73:497–511.
135. Delaunois N., Sheridan R., 1989. Studies on the biology of Turridae on European coasts: *Mangelia nebula* (Montagu). *Cahiers de Biologie Marine* 30:347–359.
136. 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.
137. 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.
138. Dennell R., 1934. The feeding mechanism of the cumacean crustacean *Diastylis bradyi*. *Transactions of the Royal Society of Edinburgh* 58:125–142.

139. 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.
140. 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). *Journal of Experimental Marine Biology and Ecology* 228:257–272.
141. Di Benedetto C., Parma L., Barbaglio A., Sugni M., Bonasoro F., Candia Carnevali M.D., 2014. Echinoderm regeneration: an in vitro approach using the crinoid *Antedon mediterranea*. *Cell and Tissue Research* 358:189–201.
142. Donn T.E. Jr., Croker R.A., 1983. Production ecology of *Haustorius canadensis* (Amphipoda: Haustoriidae) in southern Maine. *Developments in Hydrobiology* 19:661–667.
143. Dorgan K.M., D’Amelio C., Lindsay S.M., 2016. Strategies of burrowing in soft muddy sediments by diverse polychaetes. *Invertebrate Biology* 135:287–301.
144. Dorresteijn A.W.C., Westheide W. (editors), 1999. *Reproductive Strategies and Developmental Patterns in Annelids*. Springer, Vol 142 of *Developments in Hydrobiology*, 1st edition.
145. 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.
146. Dutertre M., Hamon D., Chevalier C., Ehrhold A., 2012. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. *ICES Journal of Marine Science* 70:294–308.
147. Duval M., 1963. The biology of *Petricola pholadiformis* Lamark (Lamellibranchiata Petricolidae). *Journal of Molluscan Studies* 35:89–100.
148. Dworschak P.C., 1998. Observations on the biology of the burrowing mud shrimps *Callinassa tyrrhena* and *C. candida* (Decapoda: Thalassinidea). *Journal of Natural History* 32:1535–1548.
149. Eckberg W.R., Hill S.D., 1996. *Chaetopterus* - Oocyte maturation, early development, and regeneration. *Marine Models Electronic Record* <http://www.mbl.edu/Biological.Bulletin/mmer.html>
150. Edwards D.C.B., Moore C.G., 2009. Reproduction in the sea pen *Funiculina quadrangularis* (Anthozoa: Pennatulacea) from the west coast of Scotland. *Estuarine, Coastal and Shelf Science* 82:161–168.
151. Ellis J.R., Rogers S.I., 2000. The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 80:127–138.
152. Elofsson R., 1961. The larvae of *Pasiphaea multidentata* (Esmark) and *Pasiphaea tarda* (Krøyer). *Sarsia* 4:43–53.
153. Emig C.C., 1982. The biology of *Phoronida*. *Advances in Marine Biology* 19:1–89.
154. Emson R.H., 1977. The feeding and consequent role of *Eulalia viridis* (O. F. Müller) (Polychaeta) in intertidal communities. *Journal of the Marine Biological Association of the United Kingdom* 57:93–96.
155. Emson R.H., Whitfield P.J., 1989. Aspects of the life history of a tide pool population of *Amphipholis squamata* (Ophiuroidea) from South Devon. *Journal of the Marine Biological Association of the United Kingdom* 69:27–41.
156. Enders H.E., 1909. A study of the life-history and habits of *Chaetopterus variopedatus* Renier et Claparede. *Journal of Morphology* 20:479–531.
157. Erdoğan-Dereli D., Çınar M.E., 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.
158. Esselink P., Zwarts L., 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Marine Ecology Progress Series* 6:243–254.
159. Eydal M., Freeman M.A., Kristmundsson A., Bambir S.H., Jónsson P.M., Helgason S., 2013. *Prosorhynchoides borealis* Bartoli, Gibson & Bray, 2013 (Digenea: Bucephalidae) Cercariae from *Abra prismatica* (Mollusca: Bivalvia) in Icelandic waters. *Journal of Helminthology* 7:34–41.
160. Eyster L.S., 1981. Observations on the growth, reproduction and feeding of the nudibranch *Armina tigrina*. *Journal of Mollusc an Studies* 47:171–181.
161. Faasse M., Stikvoort E., 2002. Mariene en estuariene vlokreeftjes van zachte bodems in het Deltagebied (Crustacea: Gammaridea). *Nederlandse Faunistische Mededelingen* 17:57–86.
162. 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.
163. 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.
164. Fahy E., Gaffney J., 2001. Growth statistics of an exploited razor clam (*Ensis siliqua*) bed at Gormanstown, Co Meath, Ireland. *Hydrobiologia* 465:139–151.
165. Falk-Petersen I.B., 1982. Breeding season and egg morphology of echinoderms in Balsfjorden, northern Norway. *Sarsia* 67:215–221.
166. FAO-MedSudMed project, 2017. FAO MedSudMed project - Web site. FAO MedSudMed Project: *Nephrops norvegicus* [online]. Rome. Updated. [Cited 24/7/2017]. <http://www.faomedsudmed.org/html/species/Nephrops%20norvegicus.html>
167. 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.
168. Farmer A.S.D., 1974. Reproduction in *Nephrops norvegicus* (Decapoda: Nephropidae). *Journal of Zoology* 174:161–183.
169. Farmer A.S.D., 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). *FAO Fisheries Synopsis* 112:1–97.
170. Fauchald K., Jumars P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology – An Annual Review* 17:193–284.

171. Fernández L., González-Gurriarán E., Freire J., 1991. Population biology of *Liocarcinus depurator* (Brachyura: Portunidae) in mussel raft culture areas in the Ria De Arousa (Galicia, Nw Spain). *Journal of the Marine Biological Association of the United Kingdom* 71:375–390.
172. Fernández M.V., Heras S., Maltagliati F., Roldán M.I., 2013. Deep genetic divergence in giant red shrimp *Aristaeomorpha foliacea* (Risso, 1827) across a wide distributional range. *Journal of Sea Research* 76:146–153.
173. Ferrand J.G., 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. *Marine Biology* 99:387–392.
174. 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.
175. Fiege D., Licher F., Mackie A.S.Y., 2000. A partial review of the European Magelonidae (Annelida: Polychaeta): *Magelona mirabilis* redifined and *Johnstoni* sp. Nov. Distinguished. *Journal of the Marine Biological Association of the United Kingdom* 80:215–234.
176. Fincham A.A., 1971. Ecology and population studies of some intertidal and sublittoral sand-dwelling amphipods. *Journal of the Marine Biological Association of the United Kingdom* 51:471–488.
177. Fish J.D., 1975. Development, hatching and brood size in *Bathyporeia pilosa* and *B. pelagica* (Crustacea: Amphipoda). *Journal of the Marine Biological Association of the United Kingdom* 55:357–368.
178. Fish J.D., Fish S., 1977. The veliger larva of *Hydrobia ulvae* with observations on the veliger of *Littorina littorea* (Mollusca: Prosobranchia). *Journal of Zoology* 182:495–503.
179. Fish J.D., Fish S., 2011. A student's guide to the seashore. Third edition. Cambridge University Press, 527 p.
180. Fish J.D., Mills A., 1979. The reproductive biology of *Corophium volutator* and *C. arenarium* (Crustacea: Amphipoda). *Journal of the Marine Biological Association of the United Kingdom* 59:355–368.
181. Fish S., 1970. The biology of *Eurydice pulchra* (Crustacea: Isopoda). *Journal of the Marine Biological Association of the United Kingdom* 50:753–768.
182. Fofonoff P.W., Ruiz G.M., Steves B., Carlton J.T., 2003. California Non-native Estuarine and Marine Organisms (Cal-NEMO) System. <http://invasions.si.edu/nemesis/>.
183. Forster G.R., 1959. The ecology of *Echinus esculentus* L.. Quantitative distribution and rate of feeding. *Journal of the Marine Biological Association of the United Kingdom* 38:361–367.
184. Franke H.D., 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.
185. Freeman S.M., Richardson C.A., Seed R., 2001. Seasonal abundance, spatial distribution, spawning and growth of *Astropecten irregularis* (Echinodermata: Asteroidea). *Estuarine, Coastal and Shelf Science* 53:39–49.
186. Fretter V., Graham A., 1954. Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *Journal of the Marine Biological Association of the United Kingdom* 33:565–585.
187. Gage J.D., Tyler P.A., 1985. Growth and recruitment of the deep-sea urchin *Echinus affinis*. *Marine Biology* 90:41–53.
188. Gage J.D., Tyler P.A., Nichols D., 1986. Reproduction and growth of *Echinus acutus* var. *norvegicus* Düben & Koren and *E. elegans* Düben & Koren on the continental slope off Scotland. *Journal of Experimental Marine Biology and Ecology* 101:61–83.
189. Galap C., Leboulenger F., Grillot J.P., 1997. Seasonal variations in biochemical constituents during the reproductive cycle of the female dog cockle *Glycymeris glycymeris*. *Marine Biology* 129:625–634.
190. 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.
191. García-Flórez L., Fernández-Rueda P., 2000. Reproductive biology of spider crab females (*Maja brachydactyla*) on the coast of Asturias (north-west Spain). *Journal of the Marine Biological Association of the United Kingdom* 80:1071–1076.
192. García-Rodríguez M., Esteban A., Perez Gil J.M., 2000. Considerations on the biology of *Plesionika edwardsi* (Brandt, 1851) (Decapoda, Caridea, Pandalidae) from experimental trap catches in the Spanish western Mediterranean Sea. *Scientia Marina* 64:369–379.
193. Garrabou J., 1999. Life-history traits of *Alcyonium acaule* and *Parazoanthus axinellae* (Cnidaria, Anthozoa), with emphasis on growth. *Marine Ecology Progress Series* 178:193–204.
194. Garwood P.R., 1982. The life-cycle and population dynamics of *Streptosyllis websteri* (polychaeta: syllidae) from a Northumberland beach. *Journal of the Marine Biological Association of the United Kingdom* 62:783–798.
195. Gaudron S.M., Haga T., Wang H., Laming S.R., Duperron S., 2016. Plasticity in reproduction and nutrition in wood-boring bivalves (*Xylophaga atlantica*) from the Mid-Atlantic Ridge. *Marine Biology* 163:213.
196. Gentil F., Dauvin J.C., Ménard F., 1990. Reproductive biology of the polychaete *Owenia fusiformis* Delle Chiaje in the Bay of Seine (eastern English Channel). *Journal of Experimental Marine Biology and Ecology* 142:13–23.
197. Gervis M.H., Sims N.A., 1992. The biology and culture of pearl oysters (Bivalvia: Pteriidae). *International Center for Living Aquatic Resources Management Studies and Reviews* 21:1–49.
198. Ghiold J., 1982. Observations on the clypeasteroid *Echinocyamus pusillus* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology* 61:57–14.
199. Giangrande A., 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanography and Marine Biology – An Annual Review* 35:305–406.
200. 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. *Marine Ecology* 14:313–327.
201. Gibbs P.E., 1968. Observations on the population of *Scoloplos armiger* at Whitstable. *Journal of the Marine Biological Association of the United Kingdom* 48:225–254.
202. Gibbs P.E., 1971. A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *Journal of the Marine Biological Association of the United Kingdom* 51:745–769.

203. Gibbs P.E., Langston W.J., Burt G.R., Pascoe P.L., 1983. *Tharyx marioni* (Polychaeta): a remarkable accumulator of arsenic. *Journal of the Marine Biological Association of the United Kingdom* 63:313–325.
204. Goddard J.H.R., 1983. The opisthobranchs of Cape Arago Oregon with notes on their natural history and a summary of benthic opisthobranchs known from Oregon. MSc thesis, University of Oregon, 73 p.
205. Goddard J.H.R., 1992. Patterns of development in nudibranch molluscs from the northeast Pacific Ocean, with regional comparisons. PhD thesis, University of Oregon, 134 p.
206. Goldberg H., 1978. An investigation of the feasibility of gooseneck barnacle mariculture (*Lepas anatifera*). MSc thesis, University of British Columbia, 108 p.
207. Goñi R., Latrouite D., 2005. Review of the biology, ecology and fisheries of *Palinurus* spp. species of European waters: *Palinurus elephas* (Fabricius, 1787) and *Palinurus mauritanicus* (Gruvel, 1911). *Cahiers de Biologie Marine* 46:127–142.
208. Gramitto M.E., Froggia C., 1998. Notes on the biology and growth of *Munida intermedia* (Anomura: Galatheidae) in the western Pomo pit (Adriatic Sea). *Journal of Natural History* 32:1553–1566.
209. Grant A., Tyler P.A., 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.
210. Greathead C.F., Donnan D.W., Mair J.M., Saunders G.R., 2007. The sea pens *Virgularia mirabilis*, *Pennatula phosphorea* and *Funiculina quadrangularis*: distribution and conservation issues in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* 87:1095–1103.
211. Grémare A., 1986. A comparative study of reproductive energetics in two populations of the terebellid polychaete *Eupolymnia nebulosa* Montagu with different reproductive modes. *Journal of Experimental Marine Biology and Ecology* 96:287–302.
212. Grémare A., Amouroux J.M., Amouroux J., 1989. Modelling of consumption and assimilation in the deposit-feeding polychaete *Eupolymnia nebulosa*. *Marine Ecology Progress Series* 4:239–248.
213. Griffiths C.L., Richardson C.A., 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* 331:91–98.
214. Gros O., Duplessis M.R., Felbeck H., 1999. Embryonic development and endosymbiont transmission mode in the symbiotic clam *Lucinoma aequizonata* (Bivalvia: lucinidae). *Invertebrate Reproduction and Development* 36:93–103.
215. Gudmundsson H., 1985. Life history patterns of polychaete species of the family Spionidae. *Journal of the Marine Biological Association of the United Kingdom* 65:93–111.
216. Guerao G., Abelló P., 1999. Morphology of the early zoeal stages of *Macropipus tuberculatus* (Roux, 1830) (Crustacea, Brachyura, Portunidae). *Journal of Plankton Research* 21:1993–2008.
217. Guerao G., Pastor E., Martin J., Andrés M., Estévez A., Grau A., Duran J., Rotllant G., 2008. The offspring development of *Maja squinado* and *M. brachydactyla* (Decapoda, Brachyura, Majidae) described from plankton collected and laboratory-reared material. *Journal of Natural History* 42:2257–2276.
218. Guérin J.P., 1972. Rapports taxonomiques et développement larvaire de *Spio decoratus* Bobretzky 1871 (Annélide Polychète). *Cahiers de Biologie Marine* 13:321–339.
219. Guillou J., Sauriau P.G., 1985. Some observations on the biology and ecology of a *Venus striatula* population in the bay of Douardenez, Brittany. *Journal of the Marine Biological Association of the United Kingdom* 65:889–900.
220. Haaland B., Schram T.A., 1983. Larval development and metamorphosis of *Ophiodromus flexuosus* (Delle Chiaje) (Hesionidae, Polychaeta). *Sarsia* 68:85–96.
221. Halpern J.A., 1970. Growth rate of the tropical sea star *Luidia senegalensis* (Lamarck). *Bulletin of Marine Science* 20:626–633.
222. Hanks R.W., 1969. The genus *Sphenia* (Pelecypoda, Mollusca) in the western North Atlantic, with observations on other Myidae. PhD thesis, University of New Hampshire, 94 p.
223. Hansen B., 1993. Aspects of feeding, growth and stage development by trochophora larvae of the boreal polychaete *Mediomastus fragile* (Rasmussen) (Capitellidae). *Journal of Experimental Marine Biology and Ecology* 166:273–288.
224. Hartnoll R., Bryant A., 2001. Growth to maturity of juveniles of the spider crabs *Hyas coarctatus* Leach and *Inachus dorsettensis* (Pennant) (Brachyura: Majidae). *Journal of Experimental Marine Biology and Ecology* 263:143–158.
225. Hartnoll R.G., 1963. The biology of Manx spider crabs. *Proceedings of the Zoological Society of London* 141:423–496.
226. Hartnoll R.G., 1968. Reproduction in the burrowing crab, *Corystes cassivelaunus* (Pennant, 1777) (Decapoda, Brachyura). *Crustaceana* 15:165–170.
227. Hartnoll R.G., 1975. The annual cycle of *Alcyonium digitatum*. *Estuarine and Coastal Marine Science* 3:71–78.
228. Hartnoll R.G., 1977. Reproductive strategy in two British species of *Alcyonium*. *Biology of Benthic Organisms*. 11th European Symposium on Marine Biology, Galway, October 1976, pp 321–328.
229. Hartnoll R.G., Mohamedeen H., 1987. Laboratory growth of the larvae of six British crabs. *Journal of Experimental Marine Biology and Ecology* 107:155–170.
230. Hayward P.J., Ryland J.S. (editors), 2017. *Handbook of the Marine Fauna of North-West Europe*. Second Edition. Oxford University Press, 785 p.
231. Heffernan P., 1985. Demography of *Pholoe minuta* (Polychaeta: Sigalionidae) in Galway Bay, west coast of Ireland, with special reference to settlement and recruitment patterns. *Marine Biology* 84:323–329.
232. Henderson P.A., Holmes R.H.A., 1987. On the population biology of the common shrimp *Crangon crangon* (L.) (Crustacea: Caridea) in the Severn Estuary and Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* 67:825–847.
233. Henderson S.M., Richardson C.A., 1994. A comparison of the age, growth rate and burrowing behaviour of the razor clams, *Ensis siliqua* and *E. ensis*. *Journal of the Marine Biological Association of the United Kingdom* 74:939–954.
234. Henkel T.P., 2008. Ecology of the obligate sponge-dwelling seastar *Ophiothrix lineata*. PhD thesis, University of North Carolina, 102 p.

235. Herbert R.J.H., 2011. Performance and habitat of the mantis shrimp *Rissoides desmaresti* (Stomatopoda: Squillidae) near the range border on the south coast of England. *Journal of Crustacean Biology* 31:416–423.
236. 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. *Journal of Sea Research* 91:45–57.
237. Hily C., 1987. Spatio-temporal variability of *Chaetozone setosa* (Malmgren) populations on an organic gradient in the Bay of Brest, France. *Journal of Experimental Marine Biology and Ecology* 112:201–216.
238. Holland N.D., Holland L.Z., 1991. The fine structure of the growth stage oocytes of a lancelet (= *Amphioxus*), *Branchiostoma lanceolatum*. *Invertebrate Reproduction and Development* 19:107–122.
239. Hollertz K., Duchêne J.C., 2001. Burrowing behaviour and sediment reworking in the heart urchin *Brissopsis lyrifera* Forbes (Spatangoida). *Marine Biology* 139:951–957.
240. 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.
241. Holthuis L.B., 1980. FAO species catalogue. Shrimps and prawns of the world: an annotated catalogue of species of interest to fisheries. FAO Fisheries Synopsis 125:1–261.
242. Holthuis L.B., 1991. FAO species catalogue. Vol. 13. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. FAO Fisheries Synopsis. No. 125, Vol. 13. Rome, 292 p.
243. Holtmann S.E., Groenewold A., Schrader K.H.M., Asjes J., Craeymeersch J.A., Duineveld G.C.A., van Bostelen A.J., van der Meer J., 1996. Atlas of the zoobenthos of the Dutch continental shelf. Ministry of Transport, Public Works and Water Management: Rijswijk, The Netherlands, 243 p.
244. Hopley D. (editor), 2011. *Encyclopedia of Modern Coral Reefs*. Springer, 1205 p.
245. Horikoshi M., 1967. Reproduction, larval features and life history of *Philine denticulata* (J. Adams) (Mollusca – Tectibranchia). *Ophelia* 4:43–84.
246. Howard A.E., Bennett D.B., 1979. The substrate preference and burrowing behaviour of juvenile lobsters (*Homarus gammarus* (L.)). *Journal of Natural History* 13:433–438.
247. Hrs-Brenko M., 2006. The basket shell, *Corbula gibba* Olivi, 1792 (Bivalve Mollusks) as a species resistant to environmental disturbances: a review. *Acta Adriatica* 47:49–64.
248. Hudon C., Lamarche G., 1989. Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. *Marine Ecology Progress Series* 52:155–168.
249. Hughes T.G., 1973. Deposit feeding in *Abra tenuis* (Bivalvia: Tellinacea). *Journal of Zoology, London* 171:499–512.
250. Humphreys W.J., 1962. Electron microscope studies on eggs of *Mytilus edulis*. *Journal of Ultrastructure Research* 7:467–487.
251. Ilano A.S., 2004. Mating, development and effects of female size on offspring number and size in the neogastropod *Buccinum isaotakii* (Kira, 1959). *Journal Molluscan Studies* 70:277–282.
252. Ilano A.S., Ito A., Fujinaga K., Nakao S., 2004. Age determination of *Buccinum isaotakii* (Gastropoda: Buccinidae) from the growth striae on operculum and growth under laboratory conditions. *Aquaculture* 242:181–195.
253. Ilano A.S., Miranda R.M.T., Fujinaga K., Nakao S., 2005. Feeding behavior and food consumption of Japanese whelk, *Buccinum isaotakii* (Neogastropoda: Buccinidae). *Fisheries Science* 71:342–349.
254. Ingle R.W., 1982. Larval and post-larval development of the slender-legged spider crab, *Macropodia rostrata* (Linnaeus) (Oxyrhyncha: Majidae: Inachinae), reared in the laboratory. *Bulletin of the British Museum (Natural History)* 42:207–225.
255. Ingle R.W., Rice A.L., 1971. The offspring development of the masked crab, *Corystes Cassivelaunus* (Pennant) (Brachyura, Corystidae), reared in the laboratory. *Crustaceana* 20:271–284.
256. Jarvis J.H., King P.E., 1972. Reproduction and development in the pycnogonid *Pycnogonum littorale*. *Marine Biology* 13:146–154.
257. Jeong S.J., Yu O.H., Suh H.L., 2009. Reproductive patterns and secondary production of *Gammaropsis japonicus* (Crustacea, Amphipoda) on the seagrass *Zostera marina* of Korea. *Hydrobiologia* 623:63–76.
258. Jirkov I., 2018. Three new species of *Thelepus* Leuckart, 1849 from Europe and a redescription of *T. cincinnatus* (Fabricius, 1780) (Annelida, Terebellidae). *ZooKeys* 759:29–56.
259. Joaquim S., Matias D., Lopes B., Arnold W.S., Gaspar M.B., 2008. The reproductive cycle of white clam *Spisula solida* (L.) (Mollusca: Bivalvia): implications for aquaculture and wild stock management. *Aquaculture* 281:43–48.
260. Johansen P.O., 1996. Reproduction and sexual maturation of the scavenging deepwater isopod *Natolana borealis* (Lilljeborg) from western Norway. *Sarsia*, 81:297–306.
261. Johnson W.S., Stevens M., Watling L., 2001. Reproduction and development of marine peracarideans. *Advances in Marine Biology* 39:105–260.
262. Jones D.A., 1970. Population densities and breeding in *Eurydice Pulchra* and *Eurydice Affinis* in Britain. *Journal of the Marine Biological Association of the United Kingdom* 50:635–655.
263. Jones M.B., Smaldon G., 1989. Aspects of the biology of a population of the cosmopolitan brittlestar *Amphipholis squamata* (Echinodermata) from the Firth of Forth, Scotland. *Journal of Natural History* 23:613–625.
264. Jones N.S., 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.
265. Kaïm-Malka R.A., 1997. Biology and life cycle of *Natoluna borealis* Lilj. 1851, a scavenging isopod from the continental slope of the Mediterranean. *Deep-Sea Research I* 44:2045–2067.
266. Kannevorff E., 1965. Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* liljeborg from the Øresund. *Ophelia* 2:305–318.
267. Kelly M.S., Hughes A.D., Cook E.J., 2007. Ecology of *Psammechinus miliaris*. In: Lawrence J.M. (editor). *Edible sea urchins: biology and ecology*. Elsevier Science, pp 287–295.

268. Kerr A.K., 1981. Aspects of the biology of *Lutraria lutraria* (L.) (Bivalvia: Mactacea). PhD thesis, University of Glasgow, 167 p.
269. Kideys A.E., 1996. Determination of age and growth of *Buccinum undatum* L. (Gastropoda) off Douglas, Isle of Man. *Helgoländer Meeresuntersuchungen* 50:353–368.
270. Kideys A.E., Nash R.D.M., Hartnoll R.G., 1993. Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 73:391–403.
271. Kim W., Abele L.G., 1988. The snapping shrimp genus *Alpheus* from the eastern Pacific (Decapoda: Caridea: Alpheidae). *Smithsonian Contributions to Zoology* 454:1–119.
272. King M.G., Butler A.J., 1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). *Marine Biology* 86:129–138.
273. Kingsley-Smith P.R., Richardson C.A., Seed R., 2003. Size-related and seasonal patterns of egg collar production in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology* 295:191–206.
274. 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.
275. Kornienko E.S., Korn O.M., 2006. The larval development of *Pagurus proximus* (Decapoda: Anomura: Paguridae) reared in the laboratory. *Journal of the Marine Biological Association of the United Kingdom* 86:369–381.
276. Kornienko E.S., Selin N.I., Korn O.M., 2017. Population and reproductive characteristics of the hermit crab *Pagurus proximus* Komai, 2000 (Decapoda: Anomura: Paguridae) in the northern part of the species range. *Journal of the Marine Biological Association of the United Kingdom* 99:101–109.
277. 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). *International Review of Hydrobiology* 90:100–121.
278. Kristensen E., Kostka, J.E., 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.
279. Kruse I., Strasser M., Thiermann F., 2004. The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *Journal of Sea Research* 51:53–62.
280. Kubo K., Shimoda K., Tamaki A., 2006. Egg size and clutch size in three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan. *Journal of the Marine Biological Association of the United Kingdom* 86:103–111.
281. Kupriyanova E., Nishi E., ten Hove H.A., Rzhavsky A.V., 2001. Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. *Oceanography and Marine Biology: An Annual Review* 39:1–102.
282. La Touche R.W., 1978. The feeding behaviour of the featherstar *Antedon bifida* (Echinodermata: Crinoidea). *Journal of the Marine Biological Association of the United Kingdom* 58:877–890.
283. Labat J.P., 1984. Cycle vie de *Philocheras trispinosus* (Hailstone) (Cragonidae: Decapoda) dans la région de Banyuls-sur-Mer (Méditerranée nord-occidentale). *Vie et Milieu* 34:9–16.
284. Lacalli T.C., 1980. A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. *Canadian Technical Report of Fisheries and Aquatic Sciences* 940:1–27.
285. Lahaye M.C., Bulteel P., Jangoux M., 1990. Dynamique de population, croissance et longévité de la comatule *Antedon bifida* Echinodermata, Crinoidea. In: De Ridder C., Dubois P., Lahaye M.C., Jangoux M. (editors). *Echinoderm Research*. Rotterdam: A, A. Balkem, pp 176–182.
286. Lahaye M.C., Jangoux M., 1985. Functional morphology of the podia and ambulacral grooves of the comatulid crinoid *Antedon bifida* (Echinodermata). *Marine Biology* 86:307–18.
287. Lammens J.J., 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Netherlands Journal of Sea Research* 3:315–382.
288. Lancaster I., 1988. *Pagurus bernhardus* (L.) – An introduction to the natural history of hermit crabs. *Field Studies* 7:189–238.
289. Landeira J.M., Lozano-Soldevila F., González-Gordillo J.I., 2009. Description of the first five larval stages of *Plesionika narval* (Fabricius, 1787) (Crustacea, Decapoda, Pandalidae) obtained under laboratory conditions. *Zootaxa* 2206:45–61.
290. Laskaridou Nott P., 1980. Reproduction in *Abra alba* (Wood) and *Abra tenuis* (Montagu) (Tellinacea: Scrobiculariidae). *Journal of the Marine Biological Association of the United Kingdom* 60:465–479.
291. Lawrence J.M. (editor), 2013. *Starfish: Biology and Ecology of the Asteroidea*. Johns Hopkins University Press, Baltimore, MD, USA, 267 p.
292. Le Foll D., 1993. Biologie et exploitation de l'araignée de mer *Maja squinado* Herbst en Manche Ouest. PhD thesis, Université de Bretagne occidentale, 501 p.
293. 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.
294. Lebour M.V., 1927. Studies of the Plymouth Brachyura. I. The rearing of crabs in captivity, with a description of the larval stages of *Inachus dorsettensis*, *Macropodia longirostris* and *Maia squinado*. *Journal of the Marine Biological Association of the United Kingdom* 14:795–814.
295. Lebour M.V., 1928. Studies of the Plymouth Brachyura. II. The larval stages of *Ebalia* and *Pinnotheres*. *Journal of the Marine Biological Association of the United Kingdom* 15:109–123.

296. Lebour M.V., 1931. The larvae of the Plymouth Galatheidæ. II. Galathea squamifera and Galathea intermedia. Journal of the Marine Biological Association of the United Kingdom 17:385–390.
297. Lebour M.V., 1933. The eggs and larvae of Turritella communis Lamarck and Aporrhais pes-pelican (L.). Journal of the Marine Biological Association of the United Kingdom 18:499–506.
298. Lebour M.V., 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. Journal of the Marine Biological Association of the United Kingdom 20:547–565.
299. Lebour M.V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. Journal of the Marine Biological Association of the United Kingdom 23:119–144.
300. Lebour M.V., 1938. The life history of Kellia Suborbicularis. Journal of the Marine Biological Association of the United Kingdom 22:447–451.
301. Lebour M.V., 1944. The larval stages of Portumnus (Crustacea Brachyura) with notes on some other genera. Journal of the Marine Biological Association of the United Kingdom 26:7–15.
302. Lee C.G., Huettel M., Hong J.S., Reise K., 2004. Carrion-feeding on the sediment surface at nocturnal low tides by the polychaete Phyllodoce mucosa. Marine Biology 145:575–583.
303. Leonard A.B., 1989. Functional response in Antedon mediterranea (Lamarck) (Echinodermata: Crinoidea): the interaction of prey concentration and current velocity on a passive suspension-feeder. Journal of Experimental Marine Biology and Ecology 127:81–103.
304. Lønning S., 1976. Reproductive cycle and ultrastructure of yolk development in some echinoderms from the Bergen area, western Norway. Sarsia 62:49–72.
305. Loosanoff V.L., Davis H.C., 1963. Rearing of bivalve mollusks. Advances in Marine Biology 1:1–136.
306. 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.
307. Luttikhuisen P.C., Honkoop P.J.C., Drent J., 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve Macoma balthica. Journal of Experimental Marine Biology and Ecology 396:156–161.
308. MacBride E.W., 1903. The development of Echinus esculentus, together with some points in the development of E. miliaris and E. acutus. Philosophical Transactions of the Royal Society of London Series B 195:285–327.
309. MacDonald J.D., Pike R.B., Williamson D.I., 1957. Larvae of the British species of Diogenes, Pagurus, Anapagurus and Lithodes (Crustacea, Decapoda). Proceedings of the Zoological Society of London 128:209–258.
310. MacGinitie G.E., 1955. Distribution and ecology of marine invertebrates of Point Barrow, Alaska. Smithsonian Miscellaneous Collections 128:1–201.
311. Mackay J., Gibson G., 1999. The influence of nurse eggs on variable offspring development in Polydora cornuta (Polychaeta: Spionidae). Invertebrate Reproduction and Development 35:167–176.
312. Mackie A.S.Y., 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. Bulletin of Marine Science 48:268–276.
313. Macquart-Moulin C., 1977. Le contrôle de l'émergence et des nages nocturnes chez les pécarides des plages de méditerranée. Eurydice affinis Hansen (Isopoda), Gastrosaccus mediterraneus Bacescu, Gastrosaccus spinifer (Goës) (Mysidacea). Journal of Experimental Marine Biology and Ecology 27:61–81.
314. Macquart-Moulin C., Kaïm-Malka R., 1994. Rythme circadien endogène d'émergence et d'activité natale chez l'isopode profond Cirolana borealis lilljeborg. Marine Behaviour and Physiology 24:151–164.
315. Maiorano P., D'Onghia G., Capezzuto F., Sion L., 2002. Life-history traits of Plesionika martia (Decapoda: Caridea) from the eastern-central Mediterranean Sea. Marine Biology 141:527–539.
316. Makra A., Keegan B.F., 1998. Microdistribution within a population of Acrocnida brachiata (Montagu), (Echinodermata: Ophiuroidea) in Little Killary, west coast of Ireland. Helgoländer Meeresuntersuchungen 52:65–73.
317. Manjón-Cabeza M.E., García Raso J.E., 2000. Reproductive aspects of females of the hermit crab Diogenes pugilator (Crustacea: Decapoda: Anomura) from southern Spain. Journal of the Marine Biological Association of the United Kingdom 80:85–93.
318. Manjón-Cabeza M.E., García-Raso J.E., 1998. Population structure and growth of the hermit crab Diogenes pugilator (Decapoda: Anomura: Diogenidae) from the northeastern Atlantic. Journal of Crustacean Biology 18:753–762.
319. Marine Ecological Surveys Limited, 2008. Marine Macrofauna Genus Trait Handbook. Marine Ecological Surveys Limited, Bath, UK, 184 p.
320. Marine Species Identification Portal. <http://species-identification.org/>
321. Markham J.C., 1968. Notes on growth-patterns and shell-utilization of the hermit crab Pagurus bernhardus (L.). Ophelia 5:189–205.
322. MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. www.marlin.ac.uk/biotic
323. Martel A., Larrivée D.H., Klein K.R., Himmelman J.H., 1986. Reproductive cycle and seasonal feeding activity of the neogastropod Buccinum undatum. Marine Biology 92:211–222.
324. Martel C., Guarini J.M., Blanchard G., Sauriau P.G., Trichet C., Robert S., Garcia-Meunier P., 2004. Invasion by the marine gastropod Ocinebrellus inornatus in France. III. Comparison of biological traits with the resident species Ocinebra erinacea. Marine Biology 146:93–102.
325. Martín A.O., de Figueroa J.M.T., Palomino-Morales R.J., 2006. Sclerites in Different Tissues of Mediterranean Echinodermata. Zoological Science 23:557–564.
326. Mathivat-Lallier M.H., Cazaux C., 1991. Life-history of Nephtys hombergii in Arcachon Bay. Estuarine, Coastal and Shelf Science 32:1–9.
327. Matthews J.B.L., Pinnoi S., 1973. Ecological studies on the deep-water pelagic community of Korsfjorden, Western Norway the species of Pasiphaea and Sergestes (Crustacea Decapoda) recorded in 1968 and 1969. Sarsia 52:123–144.

328. Mattos G., Cardoso R.S., 2012. Population dynamics of two suspension-feeding bivalves on a sheltered beach in southeastern Brazil. *Helgoland Marine Research* 66:393–400.
329. Mattson S., 1981. Burrowing and feeding of *Goniada maculata* Ørsted (Polychaeta). *Sarsia* 66:49–51.
330. Maucheline J., 1971. The biology of *Schistomysis kervillei* (Crustacea, Mysidacea). *Journal of the Marine Biological Association of the United Kingdom* 51:653–658.
331. McGaw I.J., 2005. Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer productus*. *Scientia Marina* 69:375–381.
332. McHugh D., 1993. A comparative study of reproduction and development in the polychaete family Terebellidae. *The Biological Bulletin* 185: 153–167.
333. McHugh D., Fong P.P., 2002. Do life history traits account for diversity of polychaete annelids? *Invertebrate Biology* 121:325–338.
334. Meadows P.S., Reid A., 1966. The behaviour of *Corophium volutator* (Crustacea: Amphipoda). *Journal of Zoology* 150:1966:387–399.
335. Meland K., Aas P.Ø., 2013. A taxonomical review of the Gnathophausia (Crustacea, Lophogastrida), with new records from the northern mid-Atlantic ridge. *Zootaxa* 3664:199–225.
336. 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). *Journal of Experimental Marine Biology and Ecology* 218:263–284.
337. Marine Ecosystems Research Programme Trait Explorer. https://www.marine-ecosystems.org.uk/Trait_Explorer.
338. Merrill A.S., Turner R.D., 1963. Nest building in the bivalve genera *Musculus* and *Lima*. *The Veliger* 6:55–59.
339. Migné A., Davoult D., 2002. Experimental nutrition in the soft coral *Acyonium digitatum* (Cnidaria: Octocorallia): removal rate of phytoplankton and zooplankton. *Cahiers de Biologie Marine* 43:9–16.
340. Milione M., Saucedo P., Southgate P., 2011. Sexual development, sex ratio and morphometrics of *Pteria penguin* (Bivalvia: Pteriidae), in north-eastern Australia. *Molluscan Research* 31:30–36.
341. Milione M., Southgate P., 2012. Growth of the winged pearl oyster, *Pteria Penguin*, at dissimilar sites in northeastern Australia. *Journal of Shellfish Research* 31:13–20.
342. Mohamedeen H., Hartnoll R.G.H., 1989. Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 134:1–24.
343. Montgomery E.M., Hamel J.F., Mercier A., 2017. The deep-sea neogastropod *Buccinum scalariforme*: reproduction, development and growth. *Deep Sea Research Part I: Oceanographic Research Papers* 119:24–33.
344. Moore H.B., 1935. A comparison of the biology of *Echinus esculentus* in different habitats. Part II. *Journal of the Marine Biological Association of the United Kingdom* 20:109–128.
345. Moore P.G., Cameron K.S., 1999. A note on a hitherto unreported association between *Photis longicaudata* (Crustacea: Amphipoda) and *Cerianthus lloydii* (Anthozoa: Hexacorallia). *Journal of the Marine Biological Association of the United Kingdom* 79:369–370.
346. Moore P.G., Wong Y.M., 1996. Observations on the life history of *Orchomene nanus* (Coyer) (Amphipoda: Lysianassoidea) at Millport, Scotland as deduced from baited trapping. *Journal of Experimental Marine Biology and Ecology* 195:53–70.
347. Mortimer K., Mackie A.S.Y., 2014. Morphology, feeding and behaviour of British *Magelona* (Annelida: Magelonidae), with discussions on the form and function of abdominal lateral pouches. *Memoirs of Museum Victoria* 71:177–201.
348. Morton B., 2011. The biology and functional morphology of *Arctica islandica* (Bivalvia: Arcticidae): a gerontophilic living fossil. *Marine Biology Research* 7:540–553.
349. Morys C., 2010. Erarbeitung von digitalen Steckbriefen der Familie Phyllodocidae (bis zu 17 Arten) bezogen auf die gesamte Ostsee (*Phyllococe mucosa* & *Phyllococe maculata*). BSc thesis University of Rostock.
350. Mossolin E.C., Shimizu R.M., Bueno S.L.S., 2006. Population structure of *Alpheus armillatus* (Decapoda: Alpheidae) in São Sebastião and Ilhabela in southeastern Brazil. *Journal of Crustacean Biology* 26:48–54.
351. Munday B.W., Keegan B.F., 1992. Population dynamics of *Amphiuira chiajei* (Echinodermata: Ophiuroidea) in Killary Harbour, on the west coast of Ireland. *Marine Biology* 114:595–605.
352. Muus K., 1981. Density and growth of juvenile *Amphiuira filiformis* (Ophiuroidea) in the Øresund. *Ophelia* 20:153–168.
353. Myers A.A., McGrath D., 1981. Taxonomic studies on British and Irish Amphipoda. The genus *Photis* with the re-establishment of *P. pollex* (= *P. macrocoxa*). *Journal of the Marine Biological Association of the United Kingdom* 61:759–768.
354. Myers A.A., McGrath D., 1982. Taxonomic studies on British and Irish Amphipoda. The genus *Gammaropsis*. *Journal of the Marine Biological Association of the United Kingdom* 62:93–100.
355. Myers A.A., McGrath D., 1991. The *Ampelisca diadema* group of species (Amphipoda: Gammaridea) in British and Irish waters. *Journal of the Marine Biological Association of the United Kingdom* 71:265–279.
356. Nash R.D.M., Chapman C.J., Atkinson R.J.A., Morgan P.J., 1984. Observations on the burrows and burrowing behaviour of *Calocaris macandreae* (Crustacea: Decapoda: Thalassinidea). *Journal of Zoology, London* 202:425–439.
357. Ng P.K.L., 1998. Crabs. In: Carpenter K.E., Niem V.H. (editors). *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 2, Cephalopods, crustaceans, holothurians and sharks*. Rome, FAO, pp 687–1396.
358. Nichols D., 1991. Seasonal reproductive periodicity in the European comatulid crinoid *Antedon bifida* (Pennant). In: Yanagisawa T., Yasumasu I., Oguro C., Suzuki N., Motokawa T. (editors). *Biology of Echinodermata*, pp 241–248. *Proceedings of the Seventh International Echinoderm Conference, Atami, 9-14 September 1990*. A.A. Balkema. Rotterdam.
359. Nichols J.H., Lawton P., 1978. The occurrence of the larval stages of the lobster *Homarus gammarus*, (Linnaeus, 1758) off the northeast coast of England in 1976. *ICES Journal of Marine Science* 38:234–243.

360. Nicolaidou A., 1983. Life history and productivity of *Pectinaria koreni* Malmgren (Polychaeta). *Estuarine, Coastal and Shelf Science* 17:31–43.
361. 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.
362. Noffke A., Hertweck G., Kröncke I., Wehrmann A., 2009. Particle size selection and tube structure of the polychaete *Owenia fusiformis*. *Estuarine, Coastal and Shelf Science* 81:160–168.
363. Noji C.I.M., Noji T.T., 1991. Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates. *Meeresforschung* 33:235–246.
364. O'Connor B.D.S., McGrath D., Keegan B.F., 1986. Demographic equilibrium: the case of an *Amphiura filiformis* assemblage on the west coast of Ireland. *Hydrobiologia* 142:151–158.
365. Ockelmann K.W., Muus K., 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata* (Montagu). *Ophelia* 17:1–93.
366. Ockelmann K.W., Vahl O., 1970. On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. *Ophelia* 8:275–294.
367. Oh C.W., 2011. Population biology of the swimming crab *Portunus trituberculatus* (Miers, 1876) (Decapoda, Brachyura) on the western coast of Korea, Yellow Sea. *Crustaceana* 84:1251–1267.
368. Oh C.W., Hartnoll R.G., 1999. Brood loss during incubation in *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. *Journal of Crustacean Biology* 19:467–476.
369. Oh C.W., Hartnoll R.G., 1999. Size at sexual maturity, reproductive output, and seasonal reproduction of *Philocheras trispinosus* (Decapoda) in Port Erin Bay, Isle of Man. *Journal of Crustacean Biology* 19:252–259.
370. Oldfield E., 1964. The reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). *Journal of Molluscan Studies* 36:79–120.
371. Olive P.J.W., 1975. Reproductive biology of *Eulalia viridis* (Müller) (Polychaeta: Phyllodoceidae) in the north eastern U.K.. *Journal of the Marine Biological Association of the United Kingdom* 55:313–326.
372. Olive P.J.W., 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. *Journal of the Marine Biological Association of the United Kingdom*, 57:133–150.
373. Olive P.J.W., Garwood P.R., Bentley N.G., Wright N., 1981. Reproductive success, relative abundance and population structure of two species of *Nephtys* in an estuarine beach. *Marine Biology* 63:189–196.
374. Olive P.J.W., Morgan P.J., 1991. The reproductive cycles of four British intertidal *Nephtys* species in relation to their geographical distribution (Polychaeta: Nephtyidae). *Ophelia* 5:351–361.
375. Olive P.J.W., Rees S.W., Djunaedi A., 1998. Influence of photoperiod and temperature on oocyte growth in the semelparous polychaete *Nereis (Neanthes) virens*. *Marine Ecology Progress Series* 172:169–183.
376. Oliver J.S., 1973. The vertical distribution of the infauna in a sublittoral sand-bottom. MSc thesis, California State University, Hayward, 60 p.
377. Omori M., 1971. Taxonomy and some notes on the biology of a new caridean shrimp, *Plesionika izumiae* (Decapoda, Pandalidae). *Crustaceana* 20:241–256.
378. Orsi Relini L., Relini G., 1994. Biological characteristics of *Aristeus antennatus* as highlighted by long-term observation in the Ligurian Sea. In: Life cycles and fisheries of the deep water red shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus*, Bianchini M.L., Ragonese S. (editors). Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy. N.T.R. – I.T.P.P. Special Publications, 3:27–28.
379. Othomi J., 1997. Reproductive biology and growth of the deep-water pandalid shrimp *Plesionika semilaevis* (Decapoda: Caridea). *Journal of Crustacean Biology* 17:81–89.
380. Oug E., 1977. Faunal distribution close to the sediment of a shallow marine environment. *Sarsia* 63:115–121.
381. Oug E., 1980. On feeding and behaviour of *Ophiodromus flexuosus* (Delle Chiaje) and *Nereimyra punctata* (O.F. Müller) (Polychaeta, Hesionidae). *Ophelia* 19:175–191.
382. Pandian T.J., 2016. Reproduction and Development in Aquatic Invertebrates. Volume 1. Reproduction and Development in Crustacea. CRC Press, Taylor & Francis Group, 279 p.
383. Papaspyrou S., Thessalou-Legaki M., Kristensen E., 2004. Impact of *Pestarella tyrrhena* on benthic metabolism in sediment microcosms enriched with seagrass and macroalgal detritus. *Marine Ecology Progress Series* 281:165–179.
384. Parapar J., Hutchings P.A., 2014. Redescription of *Terebellides stroemii* (Polychaeta, Trichobranchidae) and designation of a neotype. *Journal of the Marine Biological Association of the United Kingdom* 95:323–337.
385. Pavanelli C.A.M., Mossolin E.C., Mantelatto F.L., 2008. Reproductive strategy of the snapping shrimp *Alpheus armillatus* H. Milne-Edwards, 1837 in the South Atlantic: fecundity, egg features, and reproductive output. *Invertebrate Reproduction and Development* 52:123–130.
386. Peharda M., Ezgeta-Balić B., 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. *Scientia Marina* 76:59–66.
387. Pérez-Portela R., Villamor A., Almada V., 2010. Phylogeography of the sea star *Marthasterias glacialis* (Asteroidea, Echinodermata): deep genetic divergence between mitochondrial lineages in the north-western mediterranean. *Marine Biology* 157:2015–2028.
388. Perron F.E., 1978. Seasonal burrowing behavior and ecology of *Aporrhais occidentalis* (Gastropoda: Strombacea). *The Biological Bulletin* 154:463–471.
389. Persson L.E., 1989. The life-cycle and productivity of *Diastylis rathkei* (cumacea: crustacea) at three nearshore localities in the Hanö Bight, Southern Baltic. *Sarsia* 74:137–144.

390. Pescinelli R.A., Pantaleão J.A.F., Mantelatto F.L., Costa R.C., 2017. Morphological description of early zoeal stages of *Alpheus brasileiro* Anker, 2012 reared in the laboratory, including a revision of the larval morphology of the first zoeal stage of the genus *Alpheus* Fabricius, 1798 (Caridea: Alpheidae). *Zootaxa* 4269:265–276.
391. Pessani D., Godino C., 1991. Offspring development of *Philocheras trispinosus* (Hailstone, 1835) (Decapoda: Crangonidae) reared in the laboratory. *Journal of Crustacean Biology* 11:123–137.
392. Petch D.A., 1986. Selective deposit-feeding by *Lumbrineris* cf. *latreilli* (Polychaeta: Lumbrineridae), with a new method for assessing selectivity by deposit-feeding organisms. *Marine Biology* 93:443–448.
393. Petersen M.E., 1999. Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* 402:107–128.
394. Petrić M., Ferri J., Mladineo I., 2010. Growth and reproduction of *Munida rutilanti* (Decapoda: Anomura: Galatheidae) and impact of parasitism by *Pleurocrypta* sp. (Isopoda: Bopyridae) in the Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom* 90:1395–1404.
395. Pettibone M.H., 1993. Scaled polychaetes (Polynoidae) associated with ophiuroids and other invertebrates and review of species referred to *Malmgrenia McIntosh* and replaced by *Malmgreniella* Hartman, with descriptions of new taxa. *Smithsonian Contributions to Zoology*, no. 538, 92 p.
396. Philipp E.E.R., Schmidt M., Gsottbauer C., Sängler A.M., Abele D., 2008. Size- and age-dependent changes in adductor muscle swimming physiology of the scallop *Aequipecten opercularis*. *Journal of Experimental Biology* 211:2492–2501.
397. Pinn E.H., Ansell A.D., 1993. The Effect of particle size on the burying ability of the brown shrimp *Crangon crangon*. *Journal of the Marine Biological Association of the United Kingdom* 73:365–377.
398. Plyusheva 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.
399. 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. *Marine Biology Research* 9:274–284.
400. Porter M.L., 2016. Collecting and processing mysids, stygiomysids, and lophogastrids. *Journal of Crustacean Biology* 36:592–595.
401. Poutiers J.M., 1998. Bivalves. Acephala, Lamellibranchia, Pelecypoda. In: Carpenter K.E., Niem V.H. (editors). *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific, Seaweeds, corals, bivalves, and gastropods*, Rome, FAO, Volume 1, pp 123–362.
402. Price R., Warwick R.M., 1980. Temporal variations in annual production and biomass in estuarine populations of the two polychaetes, *Nephtys hombergii* and *Ampharete acutifrons*. *Journal of the Marine Biological Association of the United Kingdom* 60:481–487.
403. 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.
404. Pyefinch K.A., 1949. The larval stages of *Balanus crenatus* Bruguière. *Journal of Zoology* 118:916–923.
405. Qiu S., Yang J., Zhang X., Qu X., Wang S., Zhang P., Gong X., Zhang S., Zhang X., 2000. Reproductive biology of *Pinna pectinata*. *Journal of Fisheries of China* 2000:28–31.
406. Rabaut M., 2009. *Janice conchilega*, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, 354 p.
407. Rainbow P.S., 1984. An introduction to the biology of British littoral barnacles. *Field Studies* 6:1–51.
408. Rajool Shanis C.P., 2014. Deep sea shrimp fishery off Kerala coast with emphasis on biology and population characteristics of *Plesionika quasigrandis* Chace 1985. PhD thesis, Cochin University of Science and Technology, 228 p.
409. 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.
410. Rasmussen E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11:1–507.
411. Reardon K.M., 2006. Development, assessment, and management of a potential directed fishery for Jonah Crab, (*Cancer borealis*), in the near shore Gulf of Maine. MSc thesis, University of Maine, 136 p.
412. Reddiah K., 1962. The sexuality and spawning of *Manx pectinids*. *Journal of the Marine Biological Association of the United Kingdom* 42:683–703.
413. Rees H.L., 1983. Pollution investigations off the north-east coast of England: community structure, growth and production of benthic macrofauna. *Marine Environmental Research* 9:61–110.
414. Reeve M.R., 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon Serratus*. *Journal of the Marine Biological Association of the United Kingdom* 49:77–96.
415. Richards R.A., 1992. Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). *Journal of Experimental Marine Biology and Ecology* 156:187–197.
416. Ridgway I.D., Richardson C.A., 2011. *Arctica islandica*: the longest lived non colonial animal known to science. *Reviews in Fish Biology and Fisheries* 21:297–310.
417. Rigolet C., 2013. Diversité structurelle et fonctionnelle des peuplements sablo-vaseux de Bretagne sud: impact de l'expansion d'*Haploopsis nira*. Thèse de doctorat, université Pierre et Marie Curie, Paris, France, 320 p.
418. Risk M.J., Tunnicliffe V.J., 1978. Intertidal spiral burrows: *Paraonis fulgens* and *Spiophanes wigleyi* in the Minas Basin, Bay of Fundy. *Journal of Sedimentary Research* 48:1287–1292.
419. Roberts P.E., 1973. Larvae of *Munida subrugosa* (White), 1847, from Perseverance Harbour, Campbell Island. *Journal of the Royal Society of New Zealand* 3:393–408.

420. Rodrigues F.M.A., Lomônaco C., Christoffersen M.L., 2009. Habitat partition, and variations of size and symmetry of three sympatric species of *Alpheus* (Decapoda: Caridea) along an intertidal gradient in the southwestern Atlantic. *Journal of Crustacean Biology* 29:334–342.
421. Rodríguez O., Bahamonde R., 1986. Contribución al conocimiento de *Munida subrugosa* (White, 1847) en la XII Región, Chile. In: Arana P. (editor). *La Pesca en Chile*. Escuela de Ciencias del Mar, UCV, pp 283–296.
422. Romey W., Bullock R., Dealteris J., 1994. Rapid growth of a deep-sea wood-boring bivalve. *Continental Shelf Research* 14:1349–1359.
423. Rowden A.A., 1993. The burrowing mud shrimp *Callianassa subterranea* (Decapoda) and bioturbation in the North Sea. PhD thesis, University of Plymouth, 166 p.
424. Rowden A.A., Jones M.B., 1995. The burrow structure of the mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea) from the North Sea. *Journal of Natural History* 29:1155–1165.
425. Ruppert E.E., Fox R.S., Barnes R.D., 2004. *Invertebrate Zoology. A functional evolutionary approach*. 7th Ed. Brooks/Cole, Thomson Learning learning, Inc., 990 p.
426. Russel F.S., 1963. *Advances in Marine Biology*. Academic Press Inc., London, 136 p.
427. Ryu D.K., Baik S.H., Park K.H., Chung E.Y., 2001. Age and growth of the pen shell, *Atrina* (*Servatrina*) *pectinata japonica*. *Korean Journal of Malacology* 17:71–78.
428. 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). *Canadian Journal of Zoology* 68:1639–1644.
429. 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.
430. Saleuddin A.S.M., 1964. The gonads and reproductive cycle of *Astarte sulcata* (Da Costa) and sexuality in *A. elliptica* (Brown). *Journal of Molluscan Studies* 36:141–148.
431. Sampedro M.P., Fernández L., Freire J., González-Gurriarán E., 1997. Fecundity and reproductive output of *Pisidia longicornis* (Decapoda, Anomura) in the ría de Arousa (galicia, NW Spain). *Crustaceana* 70:95–110.
432. San Vicente C., Sorbe, J.C., 1993. Biologie du mysidacé suprabenthique *Schistomysis parkeri* Norman, 1892 dans la zone Sud du golfe De Gascogne (Plage D’Hendaye). *Crustaceana* 65:222–252.
433. San Vicente C., Sorbe, J.C., 2013. Comparative life-histories, population dynamics and productivity of *Schistomysis* populations (Crustacea, Mysida) in European shelf environments. *Journal of Sea Research* 81:13–32.
434. Santana J.I., González J.A., Lozano I.J., Tuset V.M., 1997. Life history of *Plesionika edwardsi* (Crustacea, Decapoda, Pandalidae) around the Canary Islands, Eastern Central Atlantic. *South African Journal of Marine Science* 18:39–48.
435. Sanz-Brau S.A., Mezquita F., Sanz S., 1998. Seasonality in the reproductive biology of a shelf-dwelling galatheid (Crustacea: Decapoda): an example from a Western Mediterranean population of *Munida iris rutlantii*. *Cahiers de Biologie Marine* 39:185–195.
436. Sardá R., Martin D., 1993. Populations of *Streblospio* (Polychaeta: Spionidae) in temperate zones: demography and production. *Journal of the Marine Biological Association of the United Kingdom* 73:769–784.
437. Sartori A.F., Domaneschi O., 2005. The functional morphology of the Antarctic bivalve *Thracia meridionalis* Smith, 1885 (Anomalodesmata: Thraciidae). *Journal of Molluscan Studies* 71:199–210.
438. Sarvala J., 1971. Ecology of *Harmothoe sarsi* (Malmgren) (Polychaeta, Polynoidae) in the northern Baltic area. *Annales Zoologici Fennici* 8:231–309.
439. Sastry A.N., 1977. The larval development of the Jonah crab, *Cancer borealis* Stimpson, 1859, under laboratory conditions (Decapoda Brachyura). *Crustaceana* 32:290–303.
440. Sato M., Ozanai K., 1996. Role of jelly matrix of egg masses in fertilization of the polychaete *Lumbrineris latreilli*. *Invertebrate Reproduction and Development* 29:185–191.
441. Saucedo C., Monteforte M., 1997. Breeding cycle of pearl oysters *Pinctada mazatlanica* and *Pteria sterna* (Bivalvia:Pteriidae) at Bahía de la paz, Baja California Sur, Mexico. *Journal of Shellfish Research* 16:103–110.
442. Saucedo C., Monteforte M., 1997. In situ growth of pearl oysters *Pinctada mazatlanica* (Hanley 1856) and *Pteria sterna* (Gould 1851) under repopulation conditions at Bahía de La Paz, Baja California Sur, Mexico. *Aquaculture Research* 28:367–378.
443. Savina M., 2004. Modélisation écologique des populations de palourdes roses (*Paphia rhomboïdes*) et d’amandes de mer (*Glycymeris glycymeris*) en Manche. Thèse de doctorat, Université d’Aix-Marseille II, France, 185 p.
444. 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.
445. Schembri P.J., 1981. Substratum preferences, burrowing and righting in *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae). *Marine Behaviour and Physiology* 8:149–161.
446. Schembri P.J., 1982. The biology of a population of *Ebalia tuberosa* (Crustacea: Decapoda: Leucosiidae) from the Clyde Sea Area. *Journal of the Marine Biological Association of the United Kingdom* 62:101–115.
447. Schöttler U., Grieshaber M., 1988. Adaptation of the polychaete worm *Scoloplos armiger* to hypoxic conditions. *Marine Biology* 99:215–222.
448. Scinto A., Benvenuto C., Cerrano C., Mori M., 2007. Seasonal cycle of *Jassa marmorata* Holmes, 1903 (Amphipoda) in the Ligurian Sea (Mediterranean, Italy). *Journal of Crustacean Biology* 27:212–216.
449. Sejr M.K., Sand M.K., Jensen K.T., Petersen J.K., Christensen P.B., Rysgaard S., 2002. Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, Northeast Greenland). *Marine Ecology Progress Series* 244:163–169.
450. Selin N.I., 2007. Shell form, growth and life span of *Astarte arctica* and *A. borealis* (Mollusca: Bivalvia) from the subtidal zone of northeastern Sakhalin. *Russian Journal of Marine Biology* 33:232–237.

451. Sewell M.A., 1994. Small size, brooding, and protandry in the apodid sea cucumber *Leptosynapta clarki*. The Biological Bulletin 187:112–123.
452. Shafee M.S., 1980. Quantitative studies on the reproduction of black scallop, *Chlamys varia* (L.) from Lanveoc area, Bay of Brest. Journal of Experimental Marine Biology and Ecology 42:171–186.
453. Shaffer P.L., 1983. Population ecology of *Heteromastus filiformis* (Polychaeta: Capitellidae). Netherlands Journal of Sea Research 17:106–125.
454. Shalla S., 2011. Identification guide to British cumaceans. NMBAQC workshop 2010, 46 p.
455. 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.
456. Sheehy M., Bannister R., Wickins J.F., Shelton P., 1999. New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). Canadian Journal of Fisheries and Aquatic Sciences 56:1904–1915.
457. Shields J.D., 1991. The reproductive ecology and fecundity of Cancer crabs. In: Wenner A., Kuris A.M. (editors). Crustacean egg production. Rotterdam, The Netherlands, Balkema pp 193–213.
458. Sikorski A.V., 2003. Laonice (Polychaeta, Spionidae) in the Arctic and the North Atlantic. Sarsia 88:316–345.
459. Smaldon G., 1972. Population structure and breeding biology of *Pisidia longicornis* and *Porcellana platycheles*. Marine Biology 17:171–179.
460. Smith K.E., Reed A.J., Thatje S., 2015. Intracapsular development and dispersal polymorphism in the predatory gastropod *Ocenebra erinaceus* (Linnaeus 1758). Helgolander Marine Research 69:249–258.
461. Sobrino I., Silva C., Sbrana M., Kaporis K., 2005. A review on the biology and fisheries of the deep water rose shrimp, *Parapenaeus longirostris*, in European Atlantic and Mediterranean waters (Decapoda, Dendrobrachiata, Penaeidae). Crustaceana 78:1153–1184.
462. Sola J.C., 1996. Population dynamics, reproduction, growth, and secondary production of the mud-snail hydrobia ulvae (Pennant). Journal of Experimental Marine Biology and Ecology 205:49–62.
463. Sousa R., Henriques P., Biscoito M., Pinto M.R., Delgado J., Dellinger T., Gouveia L., Pinho M.R., 2014. Considerations on the biology of *Plesionika narval* (Fabricius, 1787) in the Northeastern Atlantic. Turkish Journal of Fisheries and Aquatic Sciences 14:727–737.
464. Southgate P.C., Lucas J.S. (editors), 2008. The Pearl Oyster. Elsevier, Amsterdam, 574 p.
465. 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). Estuarine, Coastal and Shelf Science 74:109–118.
466. Spight T.M., Birkeland C., Lyons A., 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). Marine Biology 24:229–242.
467. Sriknshnadas B., Ramoorthi K., 1981. Studies on the life-history of *Spio filicornis* (Muller 1776). Mahasagar-Bulletin of the National Institute of Oceanography 14:303–307.
468. Stamp T.E., 2015. *Alcyonium digitatum* with *Securiflustra securifrons* on tide-swept moderately wave-exposed circalittoral rock. 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.
469. Stanczyk S.E., 1974. Life-history patterns of three estuarine brittlestars (Ophiuroidea) at Cedar Key, Florida. PhD thesis, University of Florida, 74 p.
470. Stanczyk S.E., Shaffer P.L., 1977. The salinity tolerance of *Ophiothrix angulata* (Say) (Echinodermata: Ophiuroidea) in latitudinally separate populations. Journal of Experimental Marine Biology and Ecology 29:35–43.
471. Stecher H.J., 1968. Zur Organisation und Fortpflanzung von *Pisione remota* (Southern) (Polychaeta, Pisionidae). Zeitschrift für Morphologie und Ökologie der Tiere 61:347–410.
472. Stephen A.C., 1928. Notes on the biology of *Tellina tenuis* da Coasta. Journal of the Marine Biological Association of the United Kingdom 15:683–702.
473. Surugiu V., 2016. On the taxonomic status of the European *Scolelepis* (*Scolelepis*) *squamata* (Polychaeta: Spionidae), with description of a new species from southern Europe. Zootaxa 4161:151–176.
474. Surugiu V., Boltachova N.A., Lisitskaya E.V., 2018. The current status of *Eunereis longissima* (Johnston, 1840) (Polychaeta: Nereididae) in the Black Sea. Cahiers de Biologie Marine 59:61–69.
475. Tamaki A., 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal sand flat. Marine Ecology Progress Series 37:181–189.
476. Tapella F., Romero M.C., Lovrich G.A., Chizzini A., 2002. In: Paul A.J., Dawe E.G., Elnor R., Jamieson G.S., Kruse G.H., Otto R.S., Sainte-Marie B., Shirley T.C., Woodby D. (editors). Crabs in Cold Water Regions: Biology, Management, and Economics, Proceedings of the symposium Crab 2001. January 17-20, 2001, Anchorage, Alaska, USA, pp 115–134.
477. Taylor A.C., Moore P.G., 1995. The burrows and physiological adaptations to a burrowing lifestyle of *Natanolana borealis* (Isopoda: Cirolanidae). Marine Biology 123:805–814.
478. Teixidó N., Bensoussan N., Gori A., Fiorillo I., Viladrich N., 2015. Sexual reproduction and early life-history traits of the Mediterranean soft coral *Alcyonium acaule*. Marine Ecology 37:134–144.
479. Teixidó N., Garrabou J., Harmelin J.G., 2011. Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. PLoS ONE 6:e23744.
480. Thessalou-Legaki M., 1990. Advanced offspring development of *Callianassa tyrrenna* (Decapoda: Thalassinidea) and the effect of environmental factors. Journal of Crustacean Biology 10:659–666.
481. Thessalou-Legaki M., Kiortsis V., 1997. Estimation of the reproductive output of the burrowing shrimp *Callianassa tyrrenna*: a comparison of three different biometrical approaches. Marine Biology 127:435–442.
482. Thiébaud E., Lagadeuc Y., Olivier E., Dauvin J.C., Retière C., 1998. Do hydrodynamic factors affect the recruitment of marine invertebrates in a macrotidal area? Hydrobiologia 375/376:165–176.

483. Thiel M., 1997. Reproductive biology of an epibenthic amphipod (*Dyopodos monacanthus*) with extended parental care. *Journal of the Marine Biological Association of the United Kingdom* 77:1059–107.
484. 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.
485. Thompson M.L., Schaffner L.C., 2001. Population biology and secondary production of the suspension feeding polychaete *Chaetopterus* cf. *variopedatus*: implications for benthic-pelagic coupling in lower Chesapeake Bay. *Limnology and Oceanography* 46:1899–1907.
486. Thompson T.E., 1966. Studies on the reproduction of *Archidoris pseudoargus* (Rapp) (Gastropoda Opisthobranchia). *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 250:343–374.
487. Thorarindottir G.G., Jacobson L., Ragnarsson S.A., Garcia E.G., 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 Journal of Marine Science* 67:345–354.
488. Tillin H.M., 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>
489. 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.
490. Tirelli T., Dappiano M., Maiorana G., Pessani D., 2000. Intraspecific relationships of the hermit crab *Diogenes pugilator*: predation and competition. *Hydrobiologia* 439:43–48.
491. Tomaschko K.H., Wilhelm E., Bückmann D., 1997. Growth and reproduction of *Pycnogonum litorale* (Pycnogonida) under laboratory conditions. *Marine Biology* 129: 595–600.
492. Torres A.P., Palero F., Dos Santos A., Abelló P., Blanco E., Boné A., Guerao G., 2014. Larval stages of the deep-sea lobster *Polychaetes typhlops* (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology. *Helgoland Marine Research* 68:379–397.
493. Trask T., 1970. A description of laboratory-reared larvae of *Cancer productus* Randall (Decapoda, Brachyura) and a comparison to larvae of *Cancer magister* Dana. *Crustaceana* 18:133–146.
494. Trevor J.H., 1976. The burrowing activity of *Nephtys cirrosa* Ehlers (Annelida: Polychaeta). *Journal of Experimental Marine Biology and Ecology* 24:307–319.
495. Tuck I.D., Chapman C.J., Atkinson R.J.A., 1997. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. I. Growth and density. *ICES Journal of Marine Science* 54:125–135.
496. Tunberg B., 1983. Growth of *Dosinia exoleta* (L.) (Bivalvia) in Raunefjorden, western Norway. *Sarsia* 68:40–45.
497. 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.
498. Tunberg B., 1984. Aspects of the population ecology of *Lucinoma borealis* (L.) (Bivalvia) in Raunefjorden, western Norway. *Journal of Experimental Marine Biology and Ecology* 81:87–106.
499. Tunberg B., 1984. Population ecology of *Dosinia exoleta* (L.) (Bivalvia) in Raunefjorden, western Norway. *Sarsia* 69:159–168.
500. Tunberg B., 1986. Studies on the population ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassinidea). *Estuarine, coastal and Shelf Science* 22:753–765.
501. Türkay M., Stecher J., 2013. Occurrence of Pennant’s swimming crab, *Portunus latipes*, along the German North Sea coast. *Marine Biodiversity* 43:199–204.
502. Turra A., Checon H.H., Fernandez W.S., Majer A.P., Delboni C.G., Denadai M.R., Dias G.M., 2019. The importance of embayed coastal areas for the life cycle of two sympatric starfish species (Echinodermata, Asteroidea). *Estuarine, Coastal and Shelf Science* 219:128–138.
503. Tyler P.A., 1977. Seasonal variation and ecology of gametogenesis in the genus *Ophiura* (Ophiuroidea: Echinodermata) from the Bristol channel. *Journal of Experimental Marine Biology and Ecology* 30:185–197.
504. Tyler P.A., Gage J.D., 1984. Seasonal reproduction of *Echinus affinis* (Echinodermata: Echinoidea) in the Rockall Trough, northeast Atlantic Ocean. *Deep Sea Research Part A* 31:387–402.
505. Tyler P.A., Young C.M., 1998. Temperature and pressure tolerances in dispersal stages of the genus *Echinus* (Echinodermata: Echinoidea): prerequisites for deep-sea invasion and speciation. *Deep-Sea Research II* 45:253–277.
506. Vader W., 1969. Verspreiding en biologie van *Haustorius arenarius*, de zandvlokreeft, in Nederland (Crustacea, Amphipoda). *Zoologische Bijdragen* 2:49–58.
507. Valderhaug V.A., 1985. Population structure and production of *Lumbrineris fragilis* (Polychaeta: Lumbrineridae) in the Oslofjord (Norway) with a note on metal content of jaws. *Marine Biology* 1985:203–211.
508. Valentin C., Anger K., 1977. In-situ studies on the life cycle of *Diastylis rathkei* (Cumacea: Crustacea). *Marine Biology* 39:71–76.
509. van der Loeff M.M.R., Anderson L.G., Hall P.O.J., Iverfeldt Å., Josefson A.B., Sundby B., Westerlund S.F.G., 1984. The asphyxiation technique: an approach to distinguishing between molecular diffusion and biologically mediated transport at the sediment-water interface. *Limnology and Oceanography* 29:675–686.
510. 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. *Journal of Experimental Marine Biology and Ecology* 438:118–124.
511. Vansteenbrugge L., Van Ginderdeuren K., Van Regenmortel T., Hostens K., Vincx M., 2012. Larval mantis shrimp *Rissoides desmaresti* (Risso, 1816) (Stomatopoda) in the Belgian part of the North Sea. *Belgian Journal of Zoology* 142:154–158.

512. Vevers H.G., 1949. The biology of *Asterias rubens* L.: growth and reproduction. *Journal of the Marine Biological Association of the United Kingdom* 28:165–187.
513. Wahle R.A., Castro, Tully O., Cobb J.S., 2006. Chapter 8. Homarus. In: Phillips B.F. (editor). *Lobsters: Biology, Management, Aquaculture and Fisheries*. Wiley-Blackwell, pp 221–288.
514. Walting L. (editor), 1991. VIIIth International Colloquium on Amphipoda. Kluwer Academic, 299 p.
515. Warren L.M., 1979. *Mediomastus fragilis* Rasmussen (Polychaeta: Capitellidae), a species newly recorded from British Waters. *Journal of the Marine Biological Association of the United Kingdom* 59:757–760.
516. Wassnig M., Southgate P.C., 2012. Embryonic and larval development of *Pteria penguin* (Röding, 1798) (Bivalvia: Pteriidae). *Journal of Molluscan Studies* 78:134–141.
517. Wear R.G., Fielder D.R., 1985. The marine fauna of New Zealand: larvae of the brachyura (Crustacea, Decapoda). *New Zealand Oceanographic Institute Memoirs* 92:1-90.
518. Webb C.M., 1986. Post-larval development of the tellinacean bivalves *Abra alba*, *Tellina fabula* and *Donax vittatus* (Mollusca: Bivalvia), with reference to the late larva. *Journal of the Marine Biological Association of the United Kingdom* 66:749–762.
519. Webb G.E., 1919. The development of the species of *Upogebia* from Plymouth Sound. *Journal of the Marine Biological Association of the United Kingdom* 12:81–134.
520. Webb P., Wooldridge T.H., 1990. Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea: Mysidacea) in Algoa Bay, southern Africa. *Marine Ecology Progress Series* 62:73–77.
521. Weślowski J.M., Legeżyńska J., 2002. Life cycles of some Arctic amphipods. *Polish Polar Research* 23:253–264.
522. Widdicombe S., Austen M.C., Kendall M.A., Olsford F., Schaanning M.T., Dashfield S.L., Needham H.L., 2004. Importance of bioturbators for biodiversity maintenance: indirect effects of fishing disturbance. *Marine Ecology progress Series* 275:1–10.
523. Wikander P.B., 1980. Biometry and behaviour in *Abra nitida* (Müller) and *A. longicallus* (Scacchi) (Bivalvia, Tellinacea). *Sarsia* 65:255–268.
524. Wilde P.A.W.J., Berghuis E.M., Kok A., 1984. Structure and energy demand of the benthic community of the Oyster Ground, central North Sea. *Netherlands Journal of Sea Research* 18:143–159.
525. Wildish D.J., 1984. Secondary production of four sublittoral, soft-sediment amphipod populations in the Bay of Fundy. *Canadian Journal of Zoology* 62:1027–1033.
526. Williamson D.I., 1960. Larval stages of *Pasiphaea Sivado* and some other Pasiphaeidae (Decapoda). *Crustaceana* 1:331–341.
527. Wilson C.D., Boehlert G.W., 1993. Population biology of *Gnathopausia longispina* (Mysidacea: Lophogastrida) from a central North Pacific seamount. *Marine Biology* 115:537–543.
528. Wilson D.P., 1933. The larval stages of *Notomastus latericeus* Sars. *Journal of the Marine Biological Association of the United Kingdom* 18:511–518.
529. Wilson D.P., 1982. The larval development of three species of *Magelona* (Polychaeta) from localities near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 62:385–401.
530. Wilson H.W., 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science* 48:500–516.
531. Wilson J.G., 1992. Age-specific energetics of reproduction in *Nucula turgida* (Leckenby and Marshall) a bivalve with lecithotrophic larval development. *Invertebrate Reproduction and Development* 22:275–279.
532. Wilson R.S., 1988. A review of *Eteone Savigny*, 1820, *Mysta*, Malmgren, 1865 and *Hypereteone Bergström*, 1914 (POLYCHAETA: PHYLLODOCIDAE). *Memoirs of the Museum of Victoria* 49:385–431.
533. Wilson W.H. Jr., Ruff R.E., 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.
534. Witbaard R., Duineveld G.C.A., Amaro T., Bergman M.J.N., 2005. Growth trends in three bivalve species indicate climate forcing on the benthic ecosystem in the southeastern North Sea. *Climate Research* 30:29–38.
535. Woll A.K., 2003. In situ observations of ovigerous *Cancer pagurus* Linnaeus, 1758 in Norwegian waters (Brachyura, Cancridae). *Crustaceana* 76:469–478.
536. Woodson Lehane J.R., 2014. Applications of quantitative methods and chaos theory in ichnology for analysis of invertebrate behavior and evolution. PhD thesis, University of Utah, 433 p.
537. Word J.Q., 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.
538. Yamada S.B., Groth S.D., 2016. Growth and longevity of the red rock crab *Cancer productus* (Randall, 1840). *Journal of Shellfish Research* 35:1045–1051.
539. Yoda M., Aoki M., 2002. Comparative study of benthic and pelagic populations of *Bodotria similis* (Cumacea) from Izu Peninsula, southern Japan. *Journal of Crustacean Biology* 22:543–552.
540. Yonge C.M., 1951. Observations on *Sphenia binghami* Turton. *Journal of the Marine Biological Association of the United Kingdom* 30:387–392.
541. Yonow H., 1996. Gametogenesis, egg production and development in *Acteon tornatilis*. *Malacological Review Supplement* 6:31–52.
542. Yonow N., Ryland J.S., 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.
543. Yu O.H., Soh H.Y., Suh H.L., 2002. Life history and reproduction of *Synchelidium lenorostralum* (Amphipoda, Oedicerotidae) in a temperate sandy shore, southern Korea. *Journal of Crustacean Biology* 22:126–134.

544. Yurimoto T., Tanaka K., Nasu H., Matsuoka K., 2012. Influence of resuspended sediments and their surface accumulation on a pen shell *Atrina pectinata* in Ariake Bay, West Japan. *Aquaculture Science* 56:335–342.
545. Zajac R.N., 1991. Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. *Marine Ecology Progress Series* 77:197–206.
546. Zajac R.N., Whitlatch R.B., 1989. Natural and disturbance-induced demographic variation in an infaunal polychaete, *Nephtys incisa*. *Marine Ecology Progress Series* 57:89–102.
547. Zühlke R., Blome D., van Bernem K.H., Dittmann S., 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. *Senckenbergiana maritima* 29:131–138.
548. Zühlke R., Blome D., van Bernem K.H., Dittmann S., 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. *Senckenbergiana maritima* 29:131–138.

Supplement S2

Variation partitioning

Variation partitioning has been used for a long time in different research fields; Legendre and Legendre (2012) provide a very detailed description of it. This analytical procedure quantifies the amounts of variance from a response variable or matrix explained by several predictor variables or matrices (individual and combinations of those predictors). The procedure is based on partial regression. As an example, here is an illustration from our Dutch case study. We chose the recoverability component RE based on absolute number of taxa given its pertinence: it is strongly correlated with both environmental variables ($R^2_{\text{adj.}} = 0.65$) and trawling intensity ($R^2_{\text{adj.}} = 0.47$). Figure S2.1 displays the relationships between the raw data (trawling and abiotic data \ln -transformed).

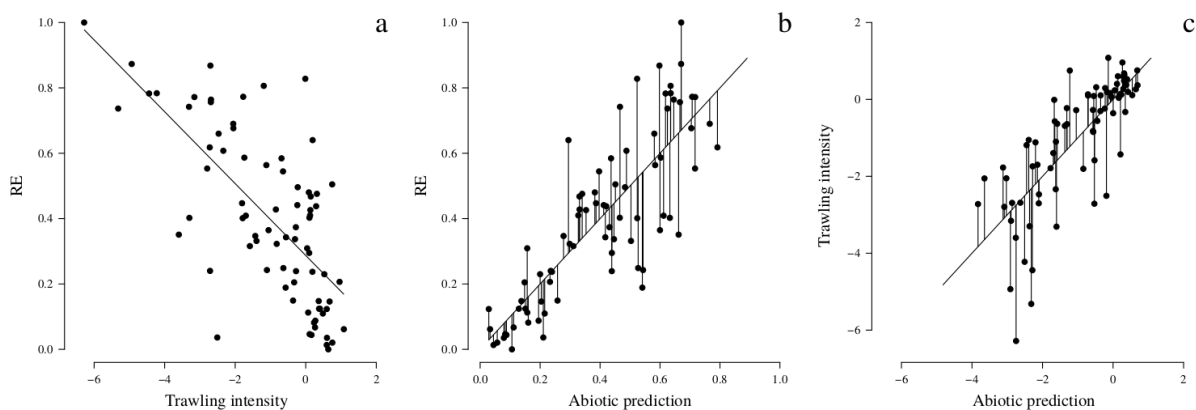


Fig. S2.1. Relationships between recoverability (RE, based on absolute taxon density), trawling intensity and abiotic variables. In b and c, abiotic prediction is the predicted value from the multiple regression of RE (b) and trawling intensity (c) on abiotic descriptors; vertical segments represent residual values of these relationships.

Trawling intensity, RE and abiotic descriptors are all strongly correlated to each other. It follows that there are two possible sources of RE variation, trawling and habitat characteristics. While habitat preferences of benthic organisms are to be expected, one cannot conclude immediately that trawling does affect benthos. Here, trawling effort is distributed according to habitat characteristics (b), but the relationship in (a) does not show if trawling affects RE within a habitat (i.e. in the way one would use a controlled experiment to establish cause-effect relationships between varying levels of trawling intensity and responses of benthos within specific environments). Hence, trawling intensity and abiotic descriptors jointly explain some of the RE variance, called “confounding effect” (here, 0.45 %, Table S5.1). However, abiotic descriptors do not fully explain RE and trawling variances as indicated by residuals in (b) and (c). These residuals reflect an element of variation in which there is no environmental effect, as illustrated in Figures S2.1a and S2.1b. The two sets of residuals are used as new variables, independent of environmental effect to assess the true effect of trawling intensity (Fig. S2.2c).

As indicated in Table 2 and Table S5.1, the amount of RE variance explained by trawling intensity, when controlling for the abiotic variation, is $R^2_{\text{adj.}} = 0.02$. This very low value results from the division of the explained variance in Figure S2.2c by the total variance of RE in Figure S2.1a. Consequently, from RE (Fig. S2.1a) to RE | Abiotic prediction (Fig. S2.2c), a large amount of variance is removed: 45 % from the confounding effect plus 20 % from Abiotic prediction | trawling intensity (environmental effect independent from trawling effect, see Table S5.1), leaving only $100 - (45 + 20) = 35$ % of RE variance for which one tries to find an effect of trawling intensity, itself constrained by abiotic variables.

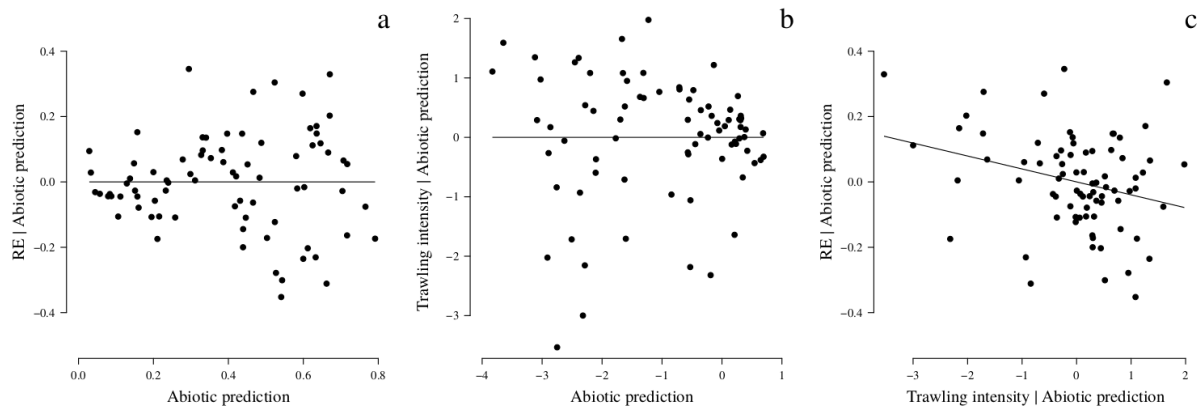


Fig. S2.2. a and b) Relationships between residual values from Figures S2.1b and S2.1c and abiotic prediction (the symbol “|” means “when controlling for”). These two sets of residuals are used in (c) to assess the response of RE to trawling intensity in the absence of abiotic interference (i.e. organism habitat preferences and habitats preferably trawled). c) Partial regression of the two variables of interest.

The greater the confounding effect, the lower the amount of explain variance that can be expected from the partial regression (Fig. S2.2c). However, the sign of variation of the final relationship is not affected by variance removal if there is a real effect, and it keeps all its functional meaning. The pure effect of trawling intensity on the response variable here, as expected according to our mechanistic rationale, is clearly negative, as indicated by the partial r -correlation coefficient equalled to -0.28 ($p = 0.009$). The very conservative nature of this approach ensures the rejection of false or unrelated effects in spite of variance removal.

References

Legendre, P., and Legendre, L. 2012. Numerical ecology, Third Edition. Elsevier, 1006 p.

Supplement S3

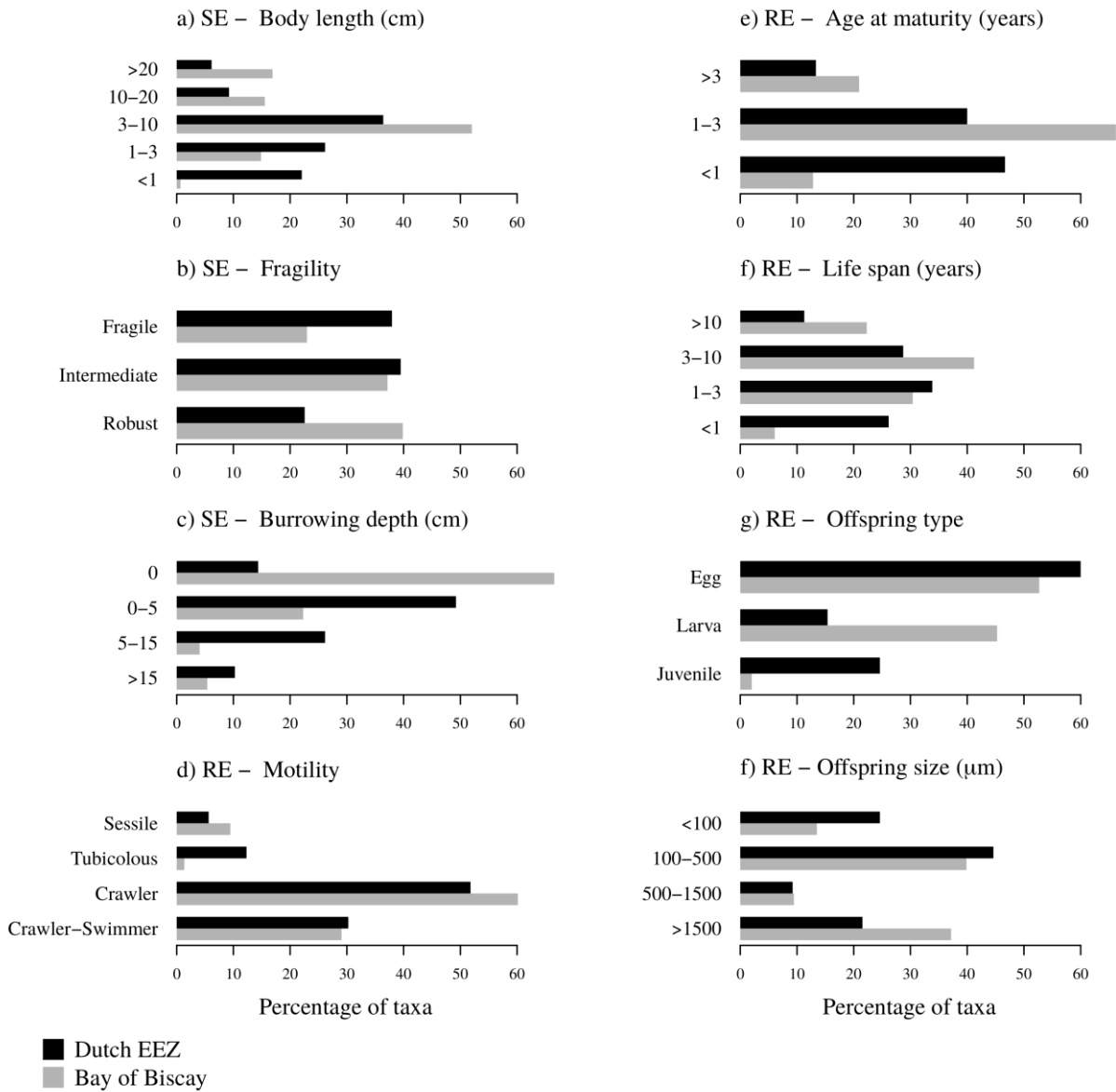


Fig. S3.1. Proportions of taxa for each biological trait modality in each of the two faunas.

Supplement S4

Table S4.1. Pearson's r correlation coefficients between traits within each case study. Rejection level: ***, $p < 0.001$; **, $p < 0.010$; *, $p < 0.050$

| | | Body length | Fragility | Burrowing depth | Motility | Age at maturity | Life span | Offspring type | Offspring size | SE |
|---------------|-----------------|-------------|-----------|-----------------|----------|-----------------|-----------|----------------|----------------|----|
| Dutch EEZ | Fragility | 0.19 ** | | | | | | | | |
| | Burrowing depth | - 0.34 *** | - 0.23 ** | | | | | | | |
| | Motility | 0.38 *** | 0.04 | 0.01 | | | | | | |
| | Age at maturity | 0.50 *** | - 0.12 | - 0.18 * | 0.27 *** | | | | | |
| | Life span | 0.48 *** | - 0.18 * | - 0.08 | 0.34 *** | 0.80 *** | | | | |
| | Offspring type | 0.59 *** | 0.07 | - 0.19 ** | 0.55 *** | 0.51 *** | 0.54 *** | | | |
| | Offspring size | 0.38 *** | 0.03 | - 0.08 | 0.57 *** | 0.45 *** | 0.47 *** | 0.81 *** | | |
| | SE | 0.47 *** | 0.58 *** | 0.20 ** | 0.20 ** | 0.12 | 0.12 | 0.29 *** | 0.18 * | |
| RE | 0.29 *** | - 0.16 * | - 0.05 | 0.46 *** | 0.68 *** | 0.54 *** | 0.33 *** | 0.41 *** | 0.02 | |
| Bay of Biscay | Fragility | - 0.04 | | | | | | | | |
| | Burrowing depth | - 0.10 | 0.12 | | | | | | | |
| | Motility | 0.13 | 0.00 | 0.17 * | | | | | | |
| | Age at maturity | 0.42 *** | - 0.05 | - 0.18 * | 0.27 ** | | | | | |
| | Life span | 0.37 *** | - 0.02 | - 0.10 | 0.33 *** | 0.73 *** | | | | |
| | Offspring type | 0.17 * | 0.27 ** | 0.19 * | 0.39 *** | 0.28 ** | 0.38 *** | | | |
| | Offspring size | 0.09 | 0.25 ** | 0.24 ** | 0.47 *** | 0.17 * | 0.29 *** | 0.82 *** | | |
| | SE | 0.36 *** | 0.80 *** | 0.30 *** | 0.05 | 0.11 | 0.08 | 0.34 *** | 0.27 ** | |
| RE | 0.22 ** | 0.06 | 0.12 | 0.64 *** | 0.63 *** | 0.52 *** | 0.45 *** | 0.46 *** | 0.13 | |

Supplement S5

Table S5.1. Complete output of variation partitioning for the Dutch EEZ. Symbols: “|”, conditional effect; “∩”, confounding effect between environmental variables and trawling intensity (intersection). AM, age at maturity; BD, burrowing depth; BL, body length; FR, fragility; LS, life span; MO, motility; OS, offspring size; OT, offspring type; RE, recoverability; SE, sensitivity. Partial *r* indicates the Pearson’s *r*-correlation coefficient between the response variable and trawling intensity when controlling for the effect of abiotic variables; it also indicates the sign of variation of the relationship.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. ∩ Trawl. | Trawl. Abio. | Partial <i>r</i> | |
|------------------|-------------------|--------------------------------|-------------------|----------|----------------|----------------|----------------|----------------|------------------|----|
| Absolute biomass | Individual traits | BL | 0.38 | 0.05 | 0.38 | 0.32 | 0.06 | ns | ns | |
| | | FR | 0.40 | ns | 0.40 | 0.38 | 0.02 | ns | ns | |
| | | BD | 0.25 | 0.06 | 0.24 | 0.19 | 0.06 | ns | ns | |
| | | MO | 0.37 | 0.07 | 0.36 | 0.29 | 0.08 | ns | ns | |
| | | AM | 0.32 | ns | 0.31 | 0.30 | 0.02 | ns | ns | |
| | | LS | 0.30 | ns | 0.30 | 0.27 | 0.04 | ns | ns | |
| | | OT | 0.34 | 0.04 | 0.34 | 0.30 | 0.05 | ns | ns | |
| | | OS | 0.27 | 0.10 | 0.28 | 0.19 | 0.08 | ns | ns | |
| | Sensitivity | BL×FR | 0.36 | 0.05 | 0.35 | 0.30 | 0.05 | ns | ns | |
| | | BL×BD | 0.25 | 0.09 | 0.24 | 0.16 | 0.09 | ns | ns | |
| | | FR×BD | 0.28 | 0.05 | 0.29 | 0.24 | 0.04 | ns | ns | |
| | | SE | 0.26 | 0.10 | 0.27 | 0.18 | 0.09 | ns | ns | |
| | Recoverability | MO×OT | 0.29 | 0.08 | 0.28 | 0.20 | 0.09 | ns | ns | |
| | | MO×OS | 0.25 | 0.13 | 0.26 | 0.13 | 0.12 | ns | ns | |
| | | OT×OS | 0.26 | 0.09 | 0.27 | 0.19 | 0.08 | ns | ns | |
| | | MO×OT×OS | 0.24 | 0.12 | 0.25 | 0.13 | 0.11 | ns | ns | |
| | | RM | 0.26 | 0.05 | 0.27 | 0.22 | 0.04 | ns | ns | |
| | | RM×MO | 0.25 | 0.06 | 0.26 | 0.20 | 0.05 | ns | ns | |
| | | RM×OT | 0.23 | 0.05 | 0.25 | 0.19 | 0.04 | ns | ns | |
| | | RM×OS | 0.19 | 0.12 | 0.23 | 0.11 | 0.08 | 0.04 | -0.24 | |
| | | RM×MO×OT | 0.23 | 0.06 | 0.25 | 0.18 | 0.05 | ns | ns | |
| | RM×MO×OS | 0.19 | 0.13 | 0.23 | 0.10 | 0.09 | 0.04 | -0.26 | | |
| | RM×OT×OS | 0.19 | 0.11 | 0.22 | 0.11 | 0.08 | 0.04 | -0.24 | | |
| | Vulnerability | RE | 0.19 | 0.13 | 0.23 | 0.10 | 0.09 | 0.04 | -0.25 | |
| | | SE+RE | 0.26 | 0.12 | 0.28 | 0.16 | 0.10 | ns | ns | |
| | Vulnerability | SE×RE | 0.23 | 0.24 | 0.26 | ns | 0.20 | 0.04 | -0.25 | |
| | | Absolute number of individuals | Individual traits | BL | 0.75 | 0.19 | 0.75 | 0.55 | 0.20 | ns |
| | FR | | | 0.67 | 0.20 | 0.66 | 0.46 | 0.20 | ns | ns |
| BD | 0.61 | | | 0.20 | 0.61 | 0.41 | 0.20 | ns | ns | |
| MO | 0.71 | | | 0.24 | 0.70 | 0.46 | 0.24 | ns | ns | |
| AM | 0.75 | | | 0.27 | 0.75 | 0.48 | 0.28 | ns | ns | |
| LS | 0.69 | | | 0.29 | 0.68 | 0.39 | 0.30 | ns | ns | |
| OT | 0.68 | | | 0.23 | 0.67 | 0.44 | 0.24 | ns | ns | |
| OS | 0.66 | | | 0.24 | 0.65 | 0.41 | 0.25 | ns | ns | |
| Sensitivity | BL×FR | | 0.74 | 0.19 | 0.74 | 0.55 | 0.19 | ns | ns | |
| | BL×BD | | 0.74 | 0.20 | 0.74 | 0.53 | 0.21 | ns | ns | |
| | FR×BD | | 0.66 | 0.19 | 0.66 | 0.47 | 0.19 | ns | ns | |
| | SE | | 0.73 | 0.18 | 0.73 | 0.54 | 0.19 | ns | ns | |
| Recoverability | MO×OT | | 0.70 | 0.26 | 0.70 | 0.44 | 0.26 | ns | ns | |
| | MO×OS | | 0.71 | 0.27 | 0.70 | 0.43 | 0.28 | ns | ns | |
| | OT×OS | | 0.69 | 0.26 | 0.68 | 0.42 | 0.26 | ns | ns | |
| | MO×OT×OS | | 0.71 | 0.29 | 0.71 | 0.42 | 0.29 | ns | ns | |
| | RM | | 0.77 | 0.24 | 0.77 | 0.53 | 0.24 | ns | ns | |
| | RM×MO | | 0.76 | 0.39 | 0.76 | 0.37 | 0.39 | ns | ns | |
| | RM×OT | | 0.76 | 0.24 | 0.75 | 0.51 | 0.25 | ns | ns | |
| | RM×OS | | 0.80 | 0.31 | 0.80 | 0.48 | 0.32 | ns | ns | |
| | RM×MO×OT | | 0.75 | 0.41 | 0.75 | 0.35 | 0.40 | ns | ns | |
| RM×MO×OS | 0.76 | | 0.47 | 0.78 | 0.31 | 0.45 | 0.02 | -0.31 | | |
| RM×OT×OS | 0.80 | | 0.31 | 0.79 | 0.48 | 0.32 | ns | ns | | |
| RE | 0.75 | | 0.47 | 0.77 | 0.30 | 0.45 | 0.02 | -0.32 | | |
| Vulnerability | SE+RE | | 0.79 | 0.29 | 0.79 | 0.50 | 0.29 | ns | ns | |
| | SE×RE | | 0.81 | 0.35 | 0.82 | 0.47 | 0.35 | ns | ns | |

Table S5.1. Continued.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. \cap Trawl. | Trawl. Abio. | Partial <i>r</i> | |
|-------------------------|-------------------|-------------------|---------|----------|----------------|----------------|---------------------|----------------|------------------|-------|
| Absolute number of taxa | Individual traits | BL | 0.71 | 0.20 | 0.71 | 0.50 | 0.21 | ns | ns | |
| | | FR | 0.66 | 0.21 | 0.65 | 0.44 | 0.21 | ns | ns | |
| | | BD | 0.61 | 0.19 | 0.61 | 0.42 | 0.18 | ns | ns | |
| | | MO | 0.73 | 0.28 | 0.73 | 0.45 | 0.28 | ns | ns | |
| | | AM | 0.65 | 0.28 | 0.65 | 0.37 | 0.28 | ns | ns | |
| | | LS | 0.64 | 0.28 | 0.64 | 0.35 | 0.29 | ns | ns | |
| | | OT | 0.68 | 0.24 | 0.67 | 0.44 | 0.24 | ns | ns | |
| | | OS | 0.66 | 0.26 | 0.66 | 0.40 | 0.26 | ns | ns | |
| | Sensitivity | BL×FR | 0.70 | 0.18 | 0.70 | 0.52 | 0.18 | ns | ns | |
| | | BL×BD | 0.68 | 0.18 | 0.68 | 0.51 | 0.18 | ns | ns | |
| | | FR×BD | 0.63 | 0.17 | 0.63 | 0.46 | 0.17 | ns | ns | |
| | | SE | 0.66 | 0.13 | 0.66 | 0.53 | 0.13 | ns | ns | |
| | Recoverability | MO×OT | 0.73 | 0.29 | 0.73 | 0.44 | 0.30 | ns | ns | |
| | | MO×OS | 0.74 | 0.32 | 0.73 | 0.42 | 0.32 | ns | ns | |
| | | OT×OS | 0.69 | 0.27 | 0.69 | 0.42 | 0.27 | ns | ns | |
| | | MO×OT×OS | 0.74 | 0.33 | 0.73 | 0.41 | 0.33 | ns | ns | |
| | | RM | 0.64 | 0.23 | 0.64 | 0.41 | 0.24 | ns | ns | |
| | | RM×MO | 0.66 | 0.41 | 0.67 | 0.26 | 0.40 | ns | ns | |
| | | RM×OT | 0.63 | 0.23 | 0.62 | 0.39 | 0.24 | ns | ns | |
| | | RM×OS | 0.68 | 0.30 | 0.67 | 0.37 | 0.31 | ns | ns | |
| | | RM×MO×OT | 0.65 | 0.42 | 0.66 | 0.24 | 0.41 | ns | ns | |
| | | RM×MO×OS | 0.66 | 0.47 | 0.68 | 0.20 | 0.45 | 0.02 | -0.28 | |
| | RE | 0.67 | 0.30 | 0.67 | 0.37 | 0.30 | ns | ns | | |
| | Vulnerability | SE+RE | 0.72 | 0.25 | 0.71 | 0.46 | 0.25 | ns | ns | |
| | | SE×RE | 0.74 | 0.37 | 0.74 | 0.37 | 0.37 | ns | ns | |
| | Relative biomass | Individual traits | BL | 0.10 | 0.05 | ns | ns | 0.06 | ns | ns |
| | | | FR | 0.36 | ns | 0.36 | 0.37 | 0.00 | ns | ns |
| | | | BD | 0.34 | ns | 0.37 | 0.34 | 0.00 | 0.03 | -0.20 |
| | | | MO | 0.55 | 0.14 | 0.55 | 0.41 | 0.14 | ns | ns |
| | | | AM | 0.10 | ns | 0.13 | 0.14 | 0.00 | ns | ns |
| LS | | | 0.19 | ns | 0.22 | 0.23 | 0.00 | ns | ns | |
| OT | | | 0.31 | ns | 0.34 | 0.35 | 0.00 | ns | ns | |
| OS | | | 0.32 | 0.06 | 0.42 | 0.36 | 0.00 | 0.11 | -0.41 | |
| Sensitivity | | BL×FR | 0.24 | 0.10 | 0.24 | 0.15 | 0.09 | ns | ns | |
| | | BL×BD | 0.25 | 0.07 | 0.30 | 0.22 | 0.03 | 0.04 | -0.27 | |
| | | FR×BD | 0.28 | 0.06 | 0.37 | 0.30 | 0.00 | 0.08 | -0.36 | |
| | | SE | 0.21 | 0.16 | 0.32 | 0.16 | 0.05 | 0.11 | -0.39 | |
| Recoverability | | MO×OT | 0.38 | 0.13 | 0.39 | 0.26 | 0.12 | ns | ns | |
| | | MO×OS | 0.32 | 0.19 | 0.39 | 0.20 | 0.12 | 0.07 | -0.33 | |
| | | OT×OS | 0.32 | 0.04 | 0.40 | 0.36 | 0.00 | 0.08 | -0.37 | |
| | | MO×OT×OS | 0.31 | 0.16 | 0.36 | 0.20 | 0.11 | 0.05 | -0.30 | |
| | | RM | 0.12 | ns | 0.18 | 0.17 | 0.00 | 0.06 | -0.28 | |
| | | RM×MO | 0.19 | ns | 0.24 | 0.21 | 0.00 | 0.06 | -0.29 | |
| | | RM×OT | 0.15 | ns | 0.21 | 0.20 | 0.00 | 0.06 | -0.29 | |
| | | RM×OS | 0.12 | 0.08 | 0.25 | 0.17 | 0.00 | 0.13 | -0.40 | |
| | | RM×MO×OT | 0.20 | ns | 0.26 | 0.23 | 0.00 | 0.06 | -0.30 | |
| | | RM×MO×OS | 0.16 | 0.10 | 0.29 | 0.18 | 0.00 | 0.12 | -0.40 | |
| RE | | 0.17 | 0.10 | 0.28 | 0.18 | 0.00 | 0.12 | -0.39 | | |
| Vulnerability | | SE+RE | 0.23 | 0.16 | 0.37 | 0.21 | 0.02 | 0.14 | -0.44 | |
| | | SE×RE | 0.14 | 0.31 | 0.29 | ns | 0.16 | 0.15 | -0.43 | |

Table S5.1. Continued.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. \cap Trawl. | Trawl. Abio. | Partial <i>r</i> | |
|--------------------------------|-------------------------|-------------------|---------|----------|----------------|----------------|---------------------|----------------|------------------|----|
| Relative number of individuals | Individual traits | BL | 0.30 | 0.10 | 0.33 | 0.23 | 0.06 | 0.04 | -0.25 | |
| | | FR | 0.22 | 0.10 | 0.26 | 0.16 | 0.06 | 0.03 | -0.24 | |
| | | BD | 0.46 | 0.06 | 0.46 | 0.40 | 0.06 | ns | ns | |
| | | MO | 0.50 | 0.05 | 0.50 | 0.44 | 0.05 | ns | ns | |
| | | AM | 0.60 | 0.16 | 0.60 | 0.44 | 0.16 | ns | ns | |
| | | LS | 0.40 | 0.21 | 0.43 | 0.21 | 0.19 | 0.03 | -0.25 | |
| | | OT | 0.32 | 0.11 | 0.35 | 0.24 | 0.09 | 0.03 | -0.23 | |
| | | OS | 0.36 | 0.12 | 0.37 | 0.25 | 0.11 | ns | ns | |
| | Sensitivity | BL×FR | 0.33 | 0.17 | 0.37 | 0.20 | 0.13 | 0.05 | -0.29 | |
| | | BL×BD | 0.49 | 0.21 | 0.53 | 0.32 | 0.17 | 0.03 | -0.28 | |
| | | FR×BD | 0.38 | 0.22 | 0.39 | 0.17 | 0.21 | ns | ns | |
| | | SE | 0.45 | 0.25 | 0.49 | 0.25 | 0.20 | 0.04 | -0.30 | |
| | Recoverability | MO×OT | 0.44 | 0.06 | 0.44 | 0.38 | 0.06 | ns | ns | |
| | | MO×OS | 0.40 | 0.05 | 0.40 | 0.36 | 0.04 | ns | ns | |
| | | OT×OS | 0.43 | 0.13 | 0.45 | 0.32 | 0.11 | ns | ns | |
| | | MO×OT×OS | 0.39 | 0.05 | 0.39 | 0.34 | 0.05 | ns | ns | |
| | | RM | 0.60 | 0.19 | 0.61 | 0.41 | 0.19 | ns | ns | |
| | | RM×MO | 0.68 | 0.27 | 0.68 | 0.42 | 0.26 | ns | ns | |
| | | RM×OT | 0.58 | 0.21 | 0.59 | 0.38 | 0.20 | ns | ns | |
| | | RM×OS | 0.60 | 0.23 | 0.61 | 0.38 | 0.22 | ns | ns | |
| | | RM×MO×OT | 0.66 | 0.28 | 0.67 | 0.39 | 0.27 | ns | ns | |
| | | RM×MO×OS | 0.64 | 0.28 | 0.65 | 0.37 | 0.27 | ns | ns | |
| | RE | 0.60 | 0.23 | 0.61 | 0.38 | 0.22 | ns | ns | | |
| | Vulnerability | SE+RE | 0.52 | 0.26 | 0.55 | 0.29 | 0.23 | 0.03 | -0.29 | |
| | | SE×RE | 0.50 | 0.23 | 0.53 | 0.29 | 0.21 | 0.02 | -0.25 | |
| | Relative number of taxa | Individual traits | BL | 0.53 | ns | 0.53 | 0.50 | 0.03 | ns | ns |
| | | | FR | 0.34 | ns | 0.34 | 0.34 | 0.00 | ns | ns |
| | | | BD | ns | ns | ns | ns | 0.01 | ns | ns |
| MO | | | 0.66 | 0.21 | 0.67 | 0.46 | 0.20 | ns | ns | |
| AM | | | 0.48 | 0.19 | 0.47 | 0.28 | 0.19 | ns | ns | |
| LS | | | 0.45 | 0.25 | 0.46 | 0.21 | 0.24 | ns | ns | |
| OT | | | 0.51 | 0.10 | 0.51 | 0.41 | 0.11 | ns | ns | |
| OS | | | 0.42 | 0.17 | 0.42 | 0.25 | 0.17 | ns | ns | |
| Sensitivity | | BL×FR | 0.48 | ns | 0.47 | 0.47 | 0.01 | ns | ns | |
| | | BL×BD | 0.63 | ns | 0.63 | 0.60 | 0.03 | ns | ns | |
| | | FR×BD | 0.26 | ns | 0.25 | 0.26 | 0.00 | ns | ns | |
| | | SE | 0.51 | ns | 0.51 | 0.51 | 0.00 | ns | ns | |
| Recoverability | | MO×OT | 0.60 | 0.22 | 0.61 | 0.39 | 0.21 | ns | ns | |
| | | MO×OS | 0.60 | 0.27 | 0.61 | 0.34 | 0.25 | ns | ns | |
| | | OT×OS | 0.53 | 0.18 | 0.53 | 0.35 | 0.18 | ns | ns | |
| | | MO×OT×OS | 0.58 | 0.27 | 0.60 | 0.33 | 0.26 | 0.02 | -0.24 | |
| | | RM | 0.35 | 0.09 | 0.34 | 0.25 | 0.10 | ns | ns | |
| | | RM×MO | 0.53 | 0.39 | 0.57 | 0.18 | 0.35 | 0.04 | -0.31 | |
| | | RM×OT | 0.27 | 0.08 | 0.26 | 0.19 | 0.09 | ns | ns | |
| | | RM×OS | 0.37 | 0.18 | 0.37 | 0.19 | 0.18 | ns | ns | |
| | | RM×MO×OT | 0.49 | 0.39 | 0.53 | 0.15 | 0.34 | 0.04 | -0.31 | |
| | | RM×MO×OS | 0.48 | 0.44 | 0.55 | 0.11 | 0.37 | 0.06 | -0.37 | |
| RE | | 0.47 | 0.44 | 0.54 | 0.10 | 0.37 | 0.07 | -0.37 | | |
| Vulnerability | | SE+RE | 0.63 | 0.15 | 0.65 | 0.50 | 0.14 | ns | ns | |
| | | SE×RE | 0.66 | 0.32 | 0.67 | 0.35 | 0.31 | ns | ns | |

Table S5.2. Complete output of variation partitioning for the Bay of Biscay. Symbols: “|”, conditional effect; “∩”, confounding effect between environmental variables and trawling intensity (intersection). AM, age at maturity; BD, burrowing depth; BL, body length; FR, fragility; LS, life span; MO, motility; OS, offspring size; OT, offspring type; RE, recoverability; SE, sensitivity. Partial *r* indicates the Pearson’s *r*-correlation coefficient between the response variable and trawling intensity when controlling for the effect of abiotic variables; it also indicates the sign of variation of the relationship.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. ∩ Trawl. | Trawl. Abio. | Partial <i>r</i> |
|--------------------------------|-------------------|-------------------|---------|----------|----------------|----------------|----------------|----------------|------------------|
| Absolute biomass | Individual traits | BL | 0.01 | 0.03 | 0.06 | 0.03 | ns | 0.04 | -0.21 |
| | | FR | 0.02 | 0.08 | 0.10 | 0.02 | 0.01 | 0.08 | -0.34 |
| | | BD | 0.03 | 0.07 | 0.11 | 0.03 | ns | 0.07 | -0.30 |
| | | MO | 0.03 | 0.08 | 0.12 | 0.04 | ns | 0.08 | -0.32 |
| | | AM | 0.03 | 0.04 | 0.08 | 0.04 | ns | 0.05 | -0.22 |
| | | LS | 0.03 | 0.04 | 0.08 | 0.04 | ns | 0.05 | -0.23 |
| | | OT | 0.03 | 0.07 | 0.10 | 0.03 | ns | 0.07 | -0.30 |
| | | OS | 0.05 | 0.09 | 0.14 | 0.05 | 0.01 | 0.08 | -0.35 |
| | Sensitivity | BL×FR | 0.02 | 0.09 | 0.10 | 0.01 | 0.01 | 0.09 | -0.36 |
| | | BL×BD | 0.03 | 0.09 | 0.11 | 0.02 | ns | 0.08 | -0.34 |
| | | FR×BD | 0.03 | 0.09 | 0.12 | 0.02 | 0.01 | 0.08 | -0.35 |
| | | SE | 0.03 | 0.09 | 0.11 | 0.02 | 0.01 | 0.09 | -0.36 |
| | Recoverability | MO×OT | 0.07 | 0.11 | 0.17 | 0.06 | 0.01 | 0.10 | -0.38 |
| | | MO×OS | 0.09 | 0.10 | 0.18 | 0.08 | 0.01 | 0.09 | -0.38 |
| | | OT×OS | 0.07 | 0.11 | 0.16 | 0.05 | 0.01 | 0.09 | -0.40 |
| | | MO×OT×OS | 0.10 | 0.12 | 0.20 | 0.09 | 0.02 | 0.10 | -0.41 |
| | | RM | 0.06 | 0.03 | 0.10 | 0.07 | ns | 0.04 | -0.19 |
| | | RM×MO | 0.07 | 0.05 | 0.13 | 0.08 | ns | 0.06 | -0.26 |
| | | RM×OT | 0.09 | 0.07 | 0.16 | 0.09 | ns | 0.07 | -0.30 |
| | | RM×OS | 0.13 | 0.07 | 0.20 | 0.13 | 0.01 | 0.06 | -0.31 |
| RM×MO×OT | | 0.11 | 0.09 | 0.19 | 0.11 | 0.01 | 0.08 | -0.35 | |
| RM×MO×OS | | 0.15 | 0.07 | 0.22 | 0.15 | 0.01 | 0.07 | -0.33 | |
| RE | 0.17 | 0.10 | 0.23 | 0.13 | 0.02 | 0.08 | -0.38 | | |
| Vulnerability | SE+RE | 0.08 | 0.12 | 0.18 | 0.06 | 0.01 | 0.11 | -0.41 | |
| | SE×RE | 0.04 | 0.06 | 0.09 | 0.03 | 0.01 | 0.05 | -0.29 | |
| Absolute number of individuals | Individual traits | BL | ns | 0.05 | 0.07 | 0.02 | ns | 0.06 | -0.22 |
| | | FR | ns | 0.08 | 0.08 | ns | ns | 0.08 | -0.28 |
| | | BD | 0.02 | 0.06 | 0.09 | 0.03 | ns | 0.07 | -0.24 |
| | | MO | ns | 0.10 | 0.11 | 0.01 | ns | 0.10 | -0.34 |
| | | AM | 0.06 | 0.05 | 0.12 | 0.07 | ns | 0.06 | -0.23 |
| | | LS | 0.03 | 0.04 | 0.08 | 0.04 | ns | 0.05 | -0.20 |
| | | OT | 0.02 | 0.07 | 0.10 | 0.02 | ns | 0.08 | -0.28 |
| | | OS | 0.03 | 0.12 | 0.14 | 0.02 | 0.01 | 0.11 | -0.38 |
| | Sensitivity | BL×FR | ns | 0.11 | 0.12 | ns | ns | 0.11 | -0.35 |
| | | BL×BD | ns | 0.10 | 0.10 | ns | ns | 0.10 | -0.32 |
| | | FR×BD | ns | 0.10 | 0.10 | ns | ns | 0.10 | -0.32 |
| | | SE | ns | 0.13 | 0.13 | ns | ns | 0.12 | -0.38 |
| | Recoverability | MO×OT | 0.02 | 0.12 | 0.14 | 0.02 | 0.01 | 0.11 | -0.38 |
| | | MO×OS | 0.03 | 0.12 | 0.14 | 0.02 | 0.01 | 0.11 | -0.37 |
| | | OT×OS | 0.04 | 0.14 | 0.17 | 0.03 | 0.01 | 0.13 | -0.43 |
| | | MO×OT×OS | 0.04 | 0.13 | 0.16 | 0.02 | 0.01 | 0.12 | -0.41 |
| | | RM | 0.15 | 0.04 | 0.20 | 0.16 | ns | 0.05 | -0.21 |
| | | RM×MO | 0.06 | 0.07 | 0.14 | 0.07 | ns | 0.08 | -0.28 |
| | | RM×OT | 0.14 | 0.10 | 0.23 | 0.13 | ns | 0.09 | -0.32 |
| | | RM×OS | 0.12 | 0.11 | 0.23 | 0.11 | 0.01 | 0.10 | -0.36 |
| RM×MO×OT | | 0.07 | 0.09 | 0.16 | 0.07 | ns | 0.09 | -0.33 | |
| RM×MO×OS | | 0.09 | 0.09 | 0.18 | 0.09 | ns | 0.08 | -0.32 | |
| RE | 0.14 | 0.14 | 0.26 | 0.12 | 0.02 | 0.12 | -0.41 | | |
| Vulnerability | SE+RE | 0.10 | 0.10 | 0.19 | 0.09 | 0.01 | 0.10 | -0.36 | |
| | SE×RE | 0.02 | 0.14 | 0.15 | 0.01 | ns | 0.14 | -0.40 | |
| | | SE×RE | 0.02 | 0.06 | 0.08 | 0.02 | ns | 0.07 | -0.32 |

Table S5.2. Continued.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. ∩ Trawl. | Trawl. Abio. | Partial <i>r</i> | |
|-------------------------|-------------------|-------------------|---------|----------|----------------|----------------|----------------|----------------|------------------|-------|
| Absolute number of taxa | Individual traits | BL | ns | 0.06 | 0.08 | 0.03 | ns | 0.07 | -0.24 | |
| | | FR | ns | 0.08 | 0.08 | ns | ns | 0.08 | -0.29 | |
| | | BD | 0.03 | 0.06 | 0.10 | 0.04 | ns | 0.06 | -0.25 | |
| | | MO | ns | 0.10 | 0.11 | ns | ns | 0.10 | -0.35 | |
| | | AM | 0.05 | 0.06 | 0.12 | 0.06 | ns | 0.07 | -0.25 | |
| | | LS | 0.03 | 0.04 | 0.09 | 0.04 | ns | 0.06 | -0.21 | |
| | | OT | 0.02 | 0.08 | 0.11 | 0.03 | ns | 0.08 | -0.29 | |
| | | OS | 0.03 | 0.13 | 0.15 | 0.02 | 0.01 | 0.12 | -0.39 | |
| | Sensitivity | BL×FR | ns | 0.11 | 0.12 | ns | ns | 0.12 | -0.36 | |
| | | BL×BD | ns | 0.10 | 0.11 | 0.01 | ns | 0.11 | -0.33 | |
| | | FR×BD | ns | 0.10 | 0.10 | ns | ns | 0.10 | -0.33 | |
| | | SE | ns | 0.13 | 0.13 | ns | ns | 0.13 | -0.39 | |
| | Recoverability | MO×OT | 0.01 | 0.12 | 0.12 | ns | 0.01 | 0.11 | -0.38 | |
| | | MO×OS | 0.02 | 0.11 | 0.12 | 0.01 | 0.01 | 0.11 | -0.38 | |
| | | OT×OS | 0.04 | 0.14 | 0.17 | 0.03 | 0.02 | 0.13 | -0.42 | |
| | | MO×OT×OS | 0.02 | 0.13 | 0.14 | ns | 0.01 | 0.12 | -0.40 | |
| | | RM | 0.12 | 0.06 | 0.19 | 0.13 | ns | 0.07 | -0.26 | |
| | | RM×MO | 0.04 | 0.07 | 0.12 | 0.04 | ns | 0.08 | -0.30 | |
| | | RM×OT | 0.11 | 0.11 | 0.22 | 0.11 | ns | 0.11 | -0.35 | |
| | | RM×OS | 0.11 | 0.12 | 0.22 | 0.09 | 0.01 | 0.11 | -0.38 | |
| | | RM×MO×OT | 0.04 | 0.09 | 0.13 | 0.04 | ns | 0.09 | -0.33 | |
| | | RM×MO×OS | 0.06 | 0.09 | 0.15 | 0.06 | ns | 0.08 | -0.33 | |
| | RM×OT×OS | 0.11 | 0.14 | 0.24 | 0.09 | 0.02 | 0.12 | -0.41 | | |
| | Vulnerability | RE | 0.06 | 0.10 | 0.15 | 0.06 | ns | 0.09 | -0.35 | |
| | | SE+RE | ns | 0.14 | 0.15 | 0.01 | ns | 0.14 | -0.41 | |
| | | SE×RE | 0.02 | 0.05 | 0.09 | 0.03 | ns | 0.06 | -0.27 | |
| | Relative biomass | Individual traits | BL | 0.10 | ns | 0.10 | 0.10 | ns | ns | ns |
| | | | FR | 0.06 | 0.06 | 0.10 | 0.04 | 0.02 | 0.04 | -0.24 |
| | | | BD | 0.08 | 0.06 | 0.11 | 0.05 | 0.03 | 0.03 | -0.24 |
| | | | MO | 0.07 | 0.05 | 0.11 | 0.06 | 0.01 | 0.04 | -0.25 |
| | | | AM | 0.10 | ns | 0.10 | 0.10 | ns | ns | ns |
| | | | LS | 0.23 | ns | 0.23 | 0.23 | ns | ns | ns |
| | | | OT | 0.16 | 0.10 | 0.22 | 0.12 | 0.04 | 0.06 | -0.33 |
| OS | | | 0.10 | 0.08 | 0.14 | 0.07 | 0.03 | 0.05 | -0.29 | |
| Sensitivity | | BL×FR | 0.04 | 0.08 | 0.10 | 0.02 | 0.02 | 0.06 | -0.28 | |
| | | BL×BD | 0.07 | 0.10 | 0.13 | 0.03 | 0.03 | 0.07 | -0.32 | |
| | | FR×BD | 0.07 | 0.07 | 0.11 | 0.05 | 0.03 | 0.04 | -0.26 | |
| | | SE | 0.05 | 0.09 | 0.11 | 0.03 | 0.02 | 0.06 | -0.29 | |
| Recoverability | | MO×OT | 0.12 | 0.08 | 0.17 | 0.09 | 0.03 | 0.05 | -0.32 | |
| | | MO×OS | 0.09 | 0.06 | 0.13 | 0.07 | 0.02 | 0.03 | -0.26 | |
| | | OT×OS | 0.14 | 0.11 | 0.20 | 0.10 | 0.04 | 0.06 | -0.34 | |
| | | MO×OT×OS | 0.12 | 0.08 | 0.16 | 0.09 | 0.03 | 0.05 | -0.30 | |
| | | RM | 0.09 | ns | 0.09 | 0.09 | ns | ns | ns | |
| | | RM×MO | 0.07 | ns | 0.07 | 0.07 | ns | ns | -0.10 | |
| | | RM×OT | 0.16 | 0.03 | 0.18 | 0.15 | 0.01 | 0.02 | -0.21 | |
| | | RM×OS | 0.16 | 0.02 | 0.17 | 0.15 | 0.01 | 0.02 | -0.19 | |
| | | RM×MO×OT | 0.11 | 0.03 | 0.14 | 0.10 | 0.01 | 0.03 | -0.23 | |
| | | RM×MO×OS | 0.13 | 0.03 | 0.15 | 0.12 | 0.01 | 0.02 | -0.20 | |
| RM×OT×OS | | 0.18 | 0.06 | 0.22 | 0.16 | 0.02 | 0.04 | -0.30 | | |
| Vulnerability | | RE | 0.14 | 0.05 | 0.17 | 0.13 | 0.02 | 0.03 | -0.26 | |
| | | SE+RE | 0.11 | 0.12 | 0.20 | 0.08 | 0.03 | 0.09 | -0.36 | |
| | | SE×RE | 0.03 | 0.04 | 0.06 | 0.02 | 0.01 | 0.03 | -0.20 | |

Table S5.2. Continued.

| Density | Component | Response variable | Abiotic | Trawling | Abio. + Trawl. | Abio. Trawl. | Abio. ∩ Trawl. | Trawl. Abio. | Partial <i>r</i> | |
|--------------------------------|-------------------------|-------------------|---------|----------|----------------|----------------|----------------|----------------|------------------|-------|
| Relative number of individuals | Individual traits | BL | 0.14 | ns | 0.14 | 0.14 | ns | 0.01 | ns | |
| | | FR | 0.04 | 0.08 | 0.11 | 0.03 | 0.01 | 0.07 | -0.28 | |
| | | BD | 0.11 | 0.03 | 0.13 | 0.10 | 0.01 | 0.03 | -0.20 | |
| | | MO | 0.08 | 0.07 | 0.14 | 0.07 | 0.02 | 0.05 | -0.29 | |
| | | AM | 0.07 | ns | 0.08 | 0.08 | ns | ns | -0.09 | |
| | | LS | 0.09 | ns | 0.09 | 0.09 | ns | ns | ns | |
| | | OT | 0.13 | 0.06 | 0.17 | 0.11 | 0.01 | 0.05 | -0.27 | |
| | | OS | 0.15 | 0.13 | 0.24 | 0.11 | 0.04 | 0.10 | -0.38 | |
| | Sensitivity | BL×FR | 0.05 | 0.15 | 0.18 | 0.04 | 0.02 | 0.13 | -0.39 | |
| | | BL×BD | 0.13 | 0.13 | 0.24 | 0.11 | 0.02 | 0.11 | -0.37 | |
| | | FR×BD | 0.04 | 0.12 | 0.13 | 0.02 | 0.02 | 0.10 | -0.35 | |
| | | SE | 0.04 | 0.17 | 0.19 | 0.02 | 0.02 | 0.15 | -0.42 | |
| | Recoverability | MO×OT | 0.08 | 0.09 | 0.14 | 0.05 | 0.03 | 0.06 | -0.31 | |
| | | MO×OS | 0.06 | 0.08 | 0.11 | 0.03 | 0.02 | 0.06 | -0.30 | |
| | | OT×OS | 0.18 | 0.16 | 0.29 | 0.13 | 0.05 | 0.11 | -0.41 | |
| | | MO×OT×OS | 0.08 | 0.10 | 0.14 | 0.05 | 0.03 | 0.07 | -0.32 | |
| | | RM | 0.13 | ns | 0.13 | 0.13 | ns | ns | ns | |
| | | RM×MO | ns | 0.02 | 0.03 | ns | ns | 0.02 | -0.17 | |
| | | RM×OT | 0.17 | 0.07 | 0.22 | 0.16 | 0.01 | 0.05 | -0.30 | |
| | | RM×OS | 0.14 | 0.09 | 0.21 | 0.12 | 0.02 | 0.07 | -0.34 | |
| | | RM×MO×OT | 0.02 | 0.05 | 0.06 | 0.02 | 0.01 | 0.04 | -0.24 | |
| | | RM×MO×OS | 0.04 | 0.05 | 0.08 | 0.04 | 0.01 | 0.04 | -0.24 | |
| | RE | 0.05 | 0.06 | 0.10 | 0.04 | 0.01 | 0.05 | -0.28 | | |
| | Vulnerability | SE+RE | 0.04 | 0.20 | 0.20 | 0.01 | 0.03 | 0.17 | -0.45 | |
| | | SE×RE | 0.02 | 0.05 | 0.07 | 0.02 | ns | 0.05 | -0.22 | |
| | Relative number of taxa | Individual traits | BL | 0.12 | 0.10 | 0.22 | 0.12 | 0.01 | 0.09 | -0.35 |
| | | | FR | 0.06 | 0.11 | 0.15 | 0.04 | 0.02 | 0.08 | -0.32 |
| | | | BD | 0.11 | 0.11 | 0.18 | 0.07 | 0.04 | 0.07 | -0.30 |
| MO | | | 0.09 | 0.10 | 0.15 | 0.05 | 0.03 | 0.06 | -0.31 | |
| AM | | | 0.09 | 0.09 | 0.15 | 0.06 | 0.03 | 0.06 | -0.31 | |
| LS | | | 0.06 | 0.02 | 0.06 | 0.05 | 0.01 | 0.01 | -0.14 | |
| OT | | | 0.16 | 0.18 | 0.27 | 0.09 | 0.06 | 0.12 | -0.42 | |
| OS | | | 0.15 | 0.17 | 0.26 | 0.09 | 0.06 | 0.11 | -0.41 | |
| Sensitivity | | BL×FR | 0.07 | 0.16 | 0.21 | 0.05 | 0.02 | 0.14 | -0.40 | |
| | | BL×BD | 0.12 | 0.20 | 0.27 | 0.07 | 0.04 | 0.15 | -0.44 | |
| | | FR×BD | 0.06 | 0.14 | 0.17 | 0.03 | 0.03 | 0.11 | -0.37 | |
| | | SE | 0.06 | 0.18 | 0.21 | 0.03 | 0.03 | 0.15 | -0.42 | |
| Recoverability | | MO×OT | 0.08 | 0.10 | 0.15 | 0.04 | 0.04 | 0.07 | -0.33 | |
| | | MO×OS | 0.07 | 0.10 | 0.13 | 0.03 | 0.03 | 0.06 | -0.31 | |
| | | OT×OS | 0.17 | 0.19 | 0.29 | 0.10 | 0.06 | 0.12 | -0.44 | |
| | | MO×OT×OS | 0.07 | 0.11 | 0.14 | 0.04 | 0.04 | 0.07 | -0.33 | |
| | | RM | 0.14 | 0.04 | 0.17 | 0.13 | 0.01 | 0.03 | -0.21 | |
| | | RM×MO | 0.03 | 0.04 | 0.06 | 0.02 | 0.01 | 0.03 | -0.20 | |
| | | RM×OT | 0.15 | 0.12 | 0.24 | 0.12 | 0.04 | 0.08 | -0.36 | |
| | | RM×OS | 0.13 | 0.12 | 0.22 | 0.10 | 0.04 | 0.09 | -0.36 | |
| | | RM×MO×OT | 0.05 | 0.06 | 0.09 | 0.03 | 0.01 | 0.04 | -0.24 | |
| | | RM×MO×OS | 0.06 | 0.05 | 0.10 | 0.04 | 0.01 | 0.04 | -0.24 | |
| RE | | 0.06 | 0.07 | 0.11 | 0.04 | 0.02 | 0.05 | -0.26 | | |
| Vulnerability | | SE+RE | 0.07 | 0.19 | 0.23 | 0.04 | 0.03 | 0.16 | -0.43 | |
| | | SE×RE | 0.03 | 0.05 | 0.08 | 0.03 | ns | 0.05 | -0.21 | |

Supplement S6

Figure S6.1. Interpolated absolute organism densities in the Dutch EEZ. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE \times RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.

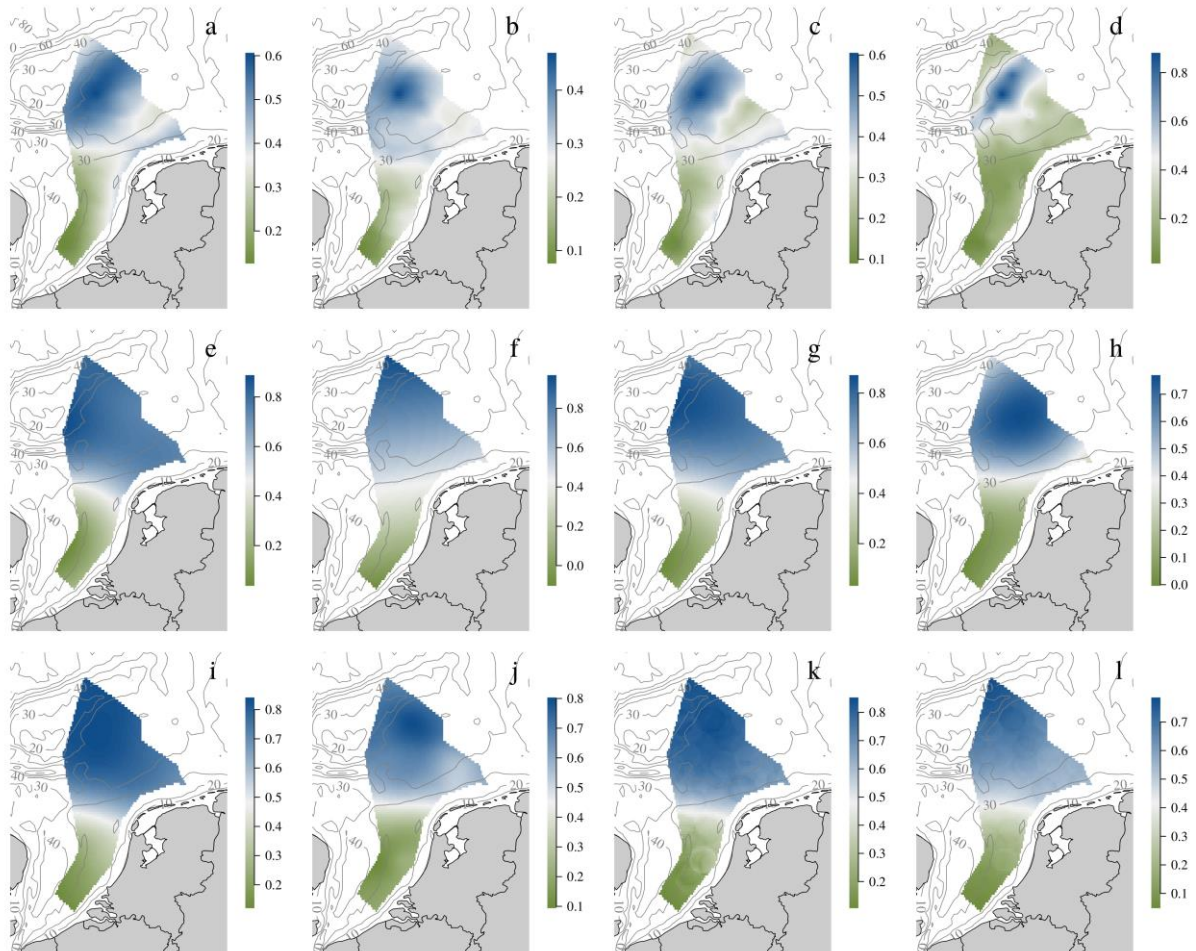


Figure S6.2. Interpolated relative organism densities in the Dutch EEZ. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE \times RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.

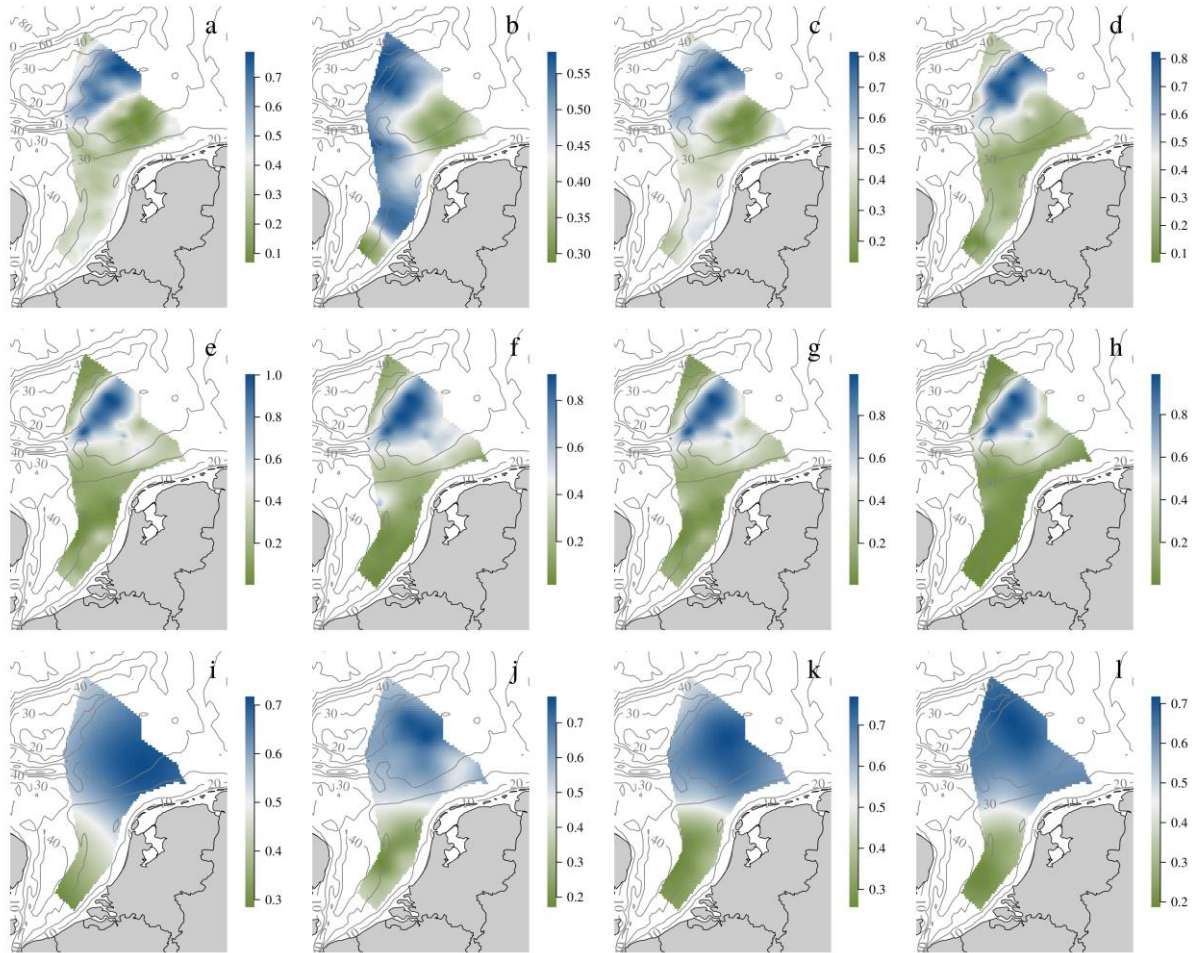


Figure S6.3. Interpolated absolute organism densities in the Bay of Biscay. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE × RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.

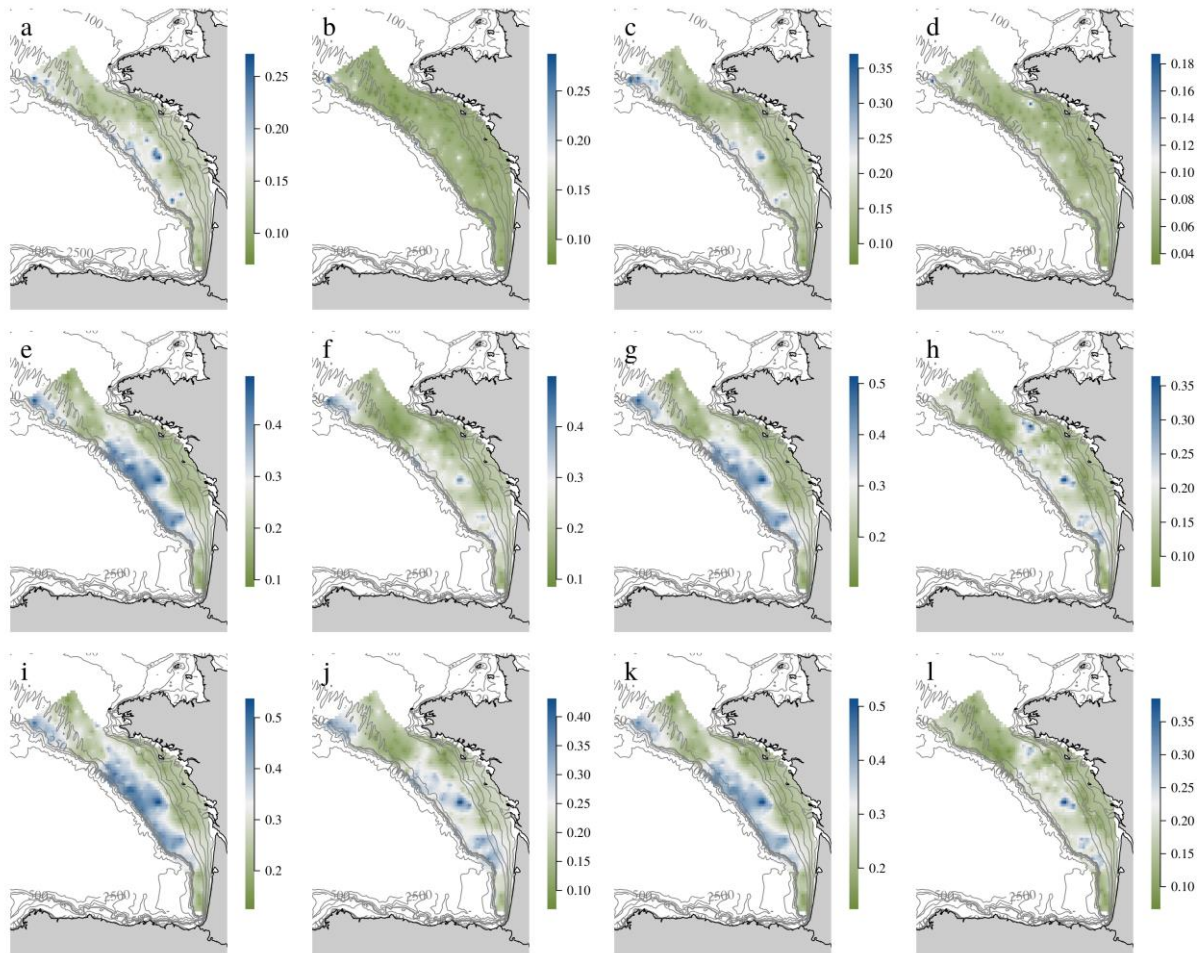


Figure S6.4. Interpolated relative organism densities in the Bay of Biscay. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE × RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.

