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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.

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
Sensitivity	Fragility	Robust	1	0.00
		Intermediate	2	0.50
		Fragile	3	1.00
	Burrowing depth (cm)	>15	1	0.00
		5-15	2	0.33
		0-5	3	0.67
		0	4	1.00
	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
Recoverability	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
	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 (mg C m^2 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).
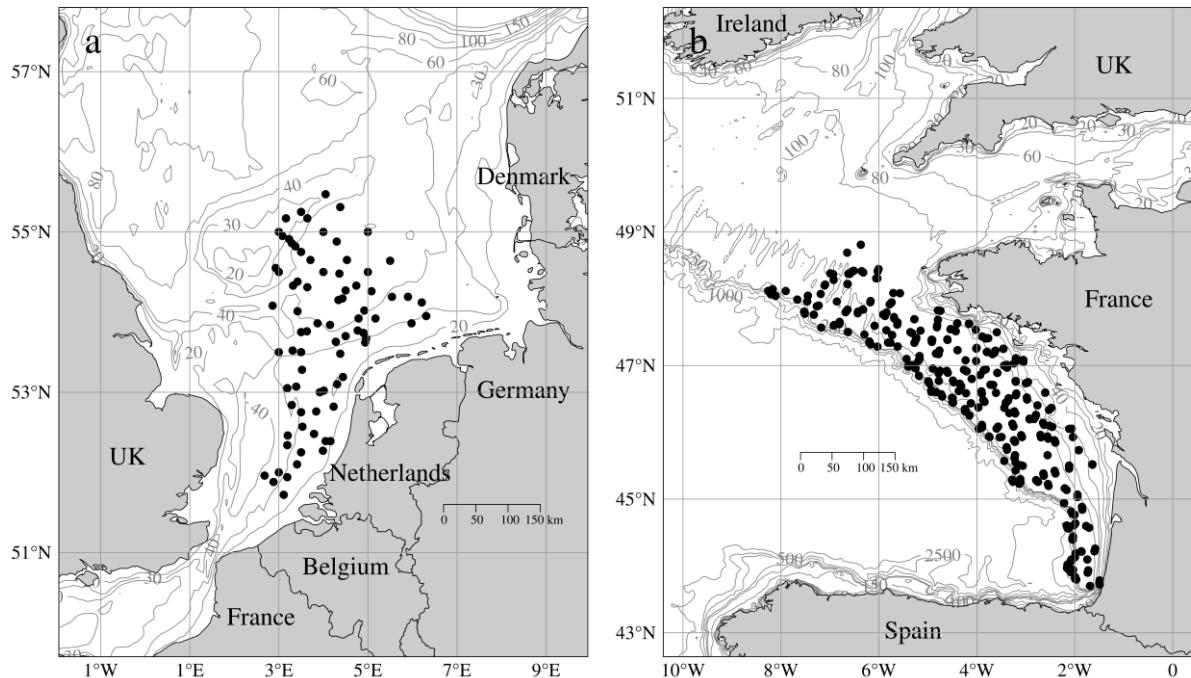
Fig. 1. Case studies. (a) Dutch exclusive economic zone (EEZ), (b) Bay of Biscay. Black dots show sampling stations; grey contours are isobaths displaying depth (m)

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 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 to relate 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 $0.05° \times 0.05°$ 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 × 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 × 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 × 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 × standardised traits matrix, generating 26 response variables, as well as the SE + RE and SE × RE variables.

Six different types of organism densities were incorporated into stations × 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).
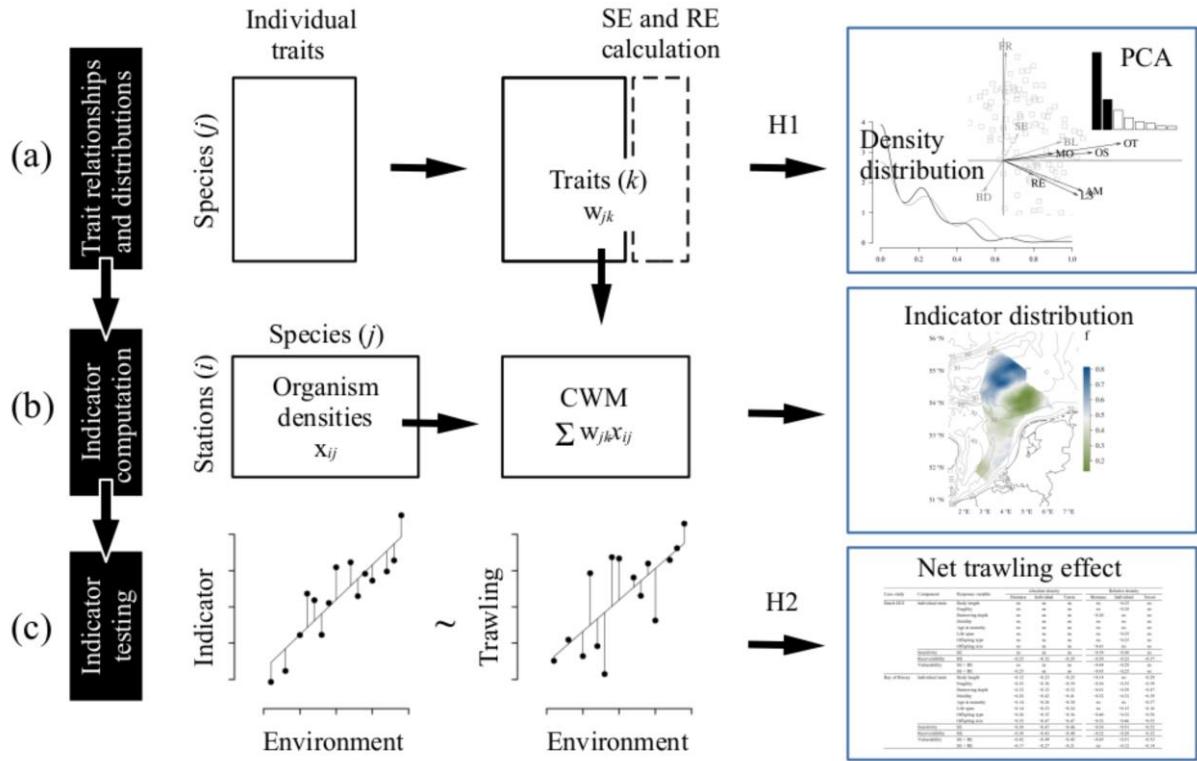

Fig. 2. Summary of data analyses. (a) Sensitivity (SE) and recoverability (RE) components are calculated from the species × individual traits matrix; PCA and distribution analyses are then used to test hypothesis 1 (H1). (b) Trait data are combined with organism densities from survey data through community 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.
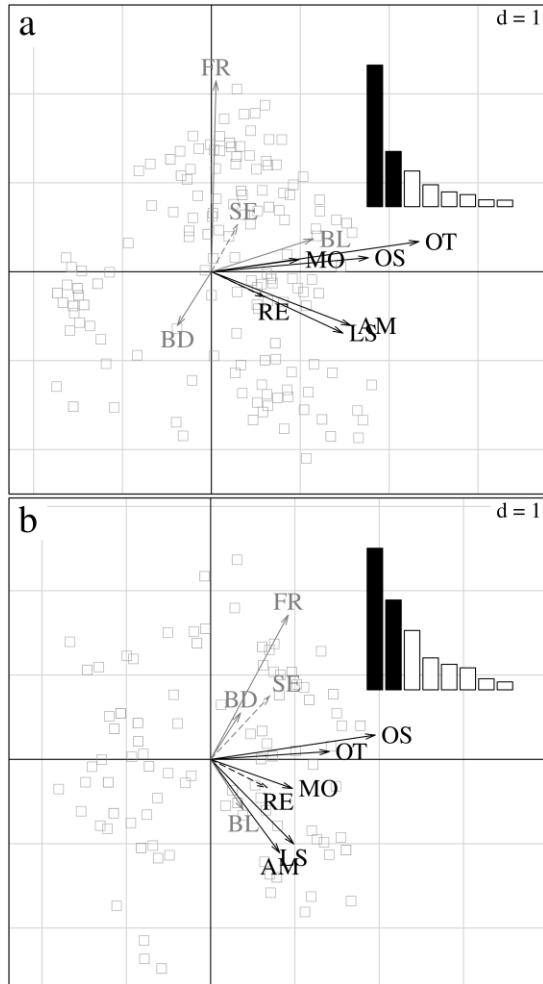
Fig. 3. Principal component analysis of biological trait covariances from taxa × standardised traits matrices. (a) Endobenthos from the Dutch EEZ. (b) Epibenthos from the Bay of Biscay. Bar diagrams, eigenvalues (black, axes 1 and 2). Grey arrows show traits of the sensitivity (SE) component; black arrows 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 × RE), both indicating slightly higher proportions of vulnerable taxa in the Bay of Biscay (Fig. 4c,d).
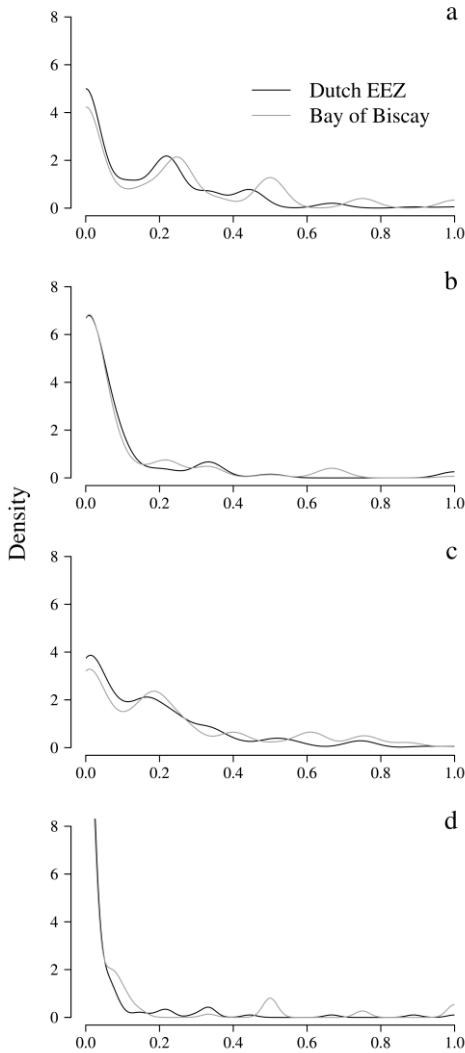
Fig. 4. Density distributions of (a) sensitivity (SE) and (b) recoverability (RE) components, and (c,d) vulnerability (SE + RE and SE × RE, respectively); x-axis, standardised indicator score. As the number of taxa differs between the 2 case studies, data are standardised in order to only compare the 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*, *Eupolymnia 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 *Callianassa* 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).
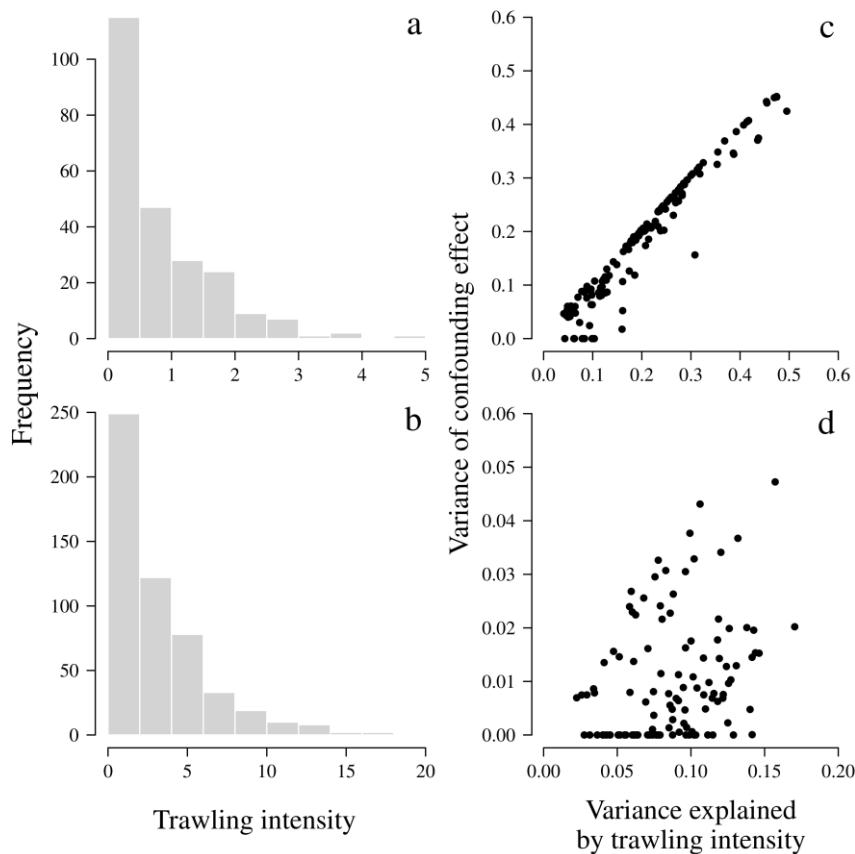
Fig. 5. Frequency distributions of trawling intensities expressed as swept area ratio for (a) the Dutch EEZ and (b) the Bay of Biscay. Also shown is the variance of response variables for individual traits and combinations of traits concurrently explained by abiotic variables and trawling intensity (confounding 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).
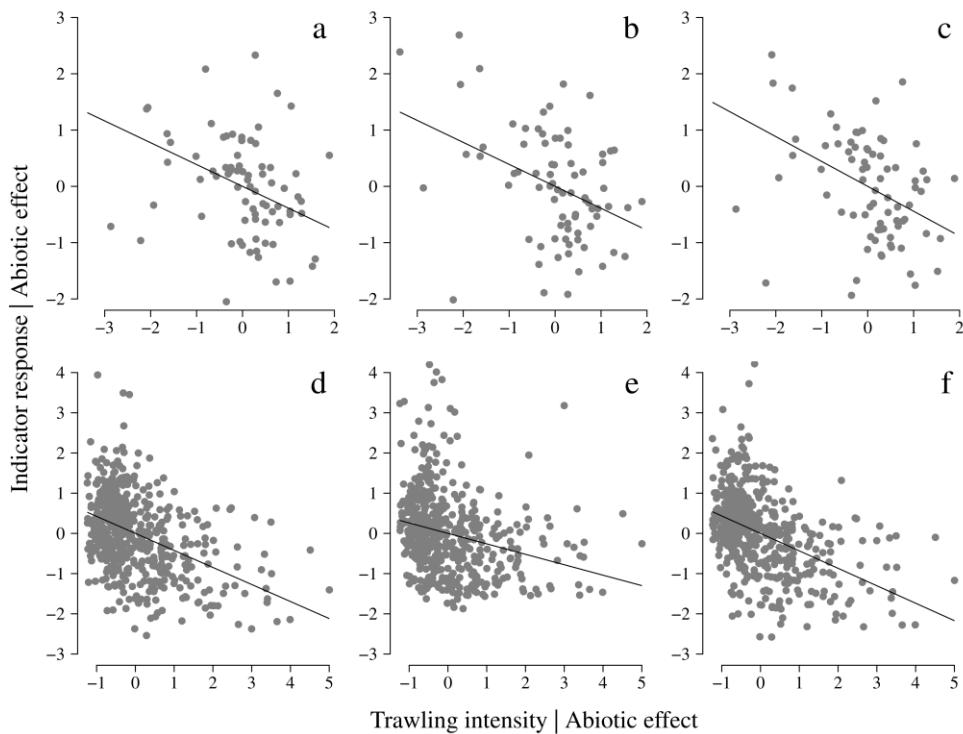
Fig. 6. Strongest indicator responses obtained for each case study. (a−c) Dutch EEZ, relative biomass density; (d−f) Bay of Biscay, relative number of taxa. Variables are standardised residuals from regression on abiotic variables (symbol '|', partial regression). (a,d) Sensitivity. (b,e) Recoverability. (c,f) Vulnerability = Sensitivity + Recoverability
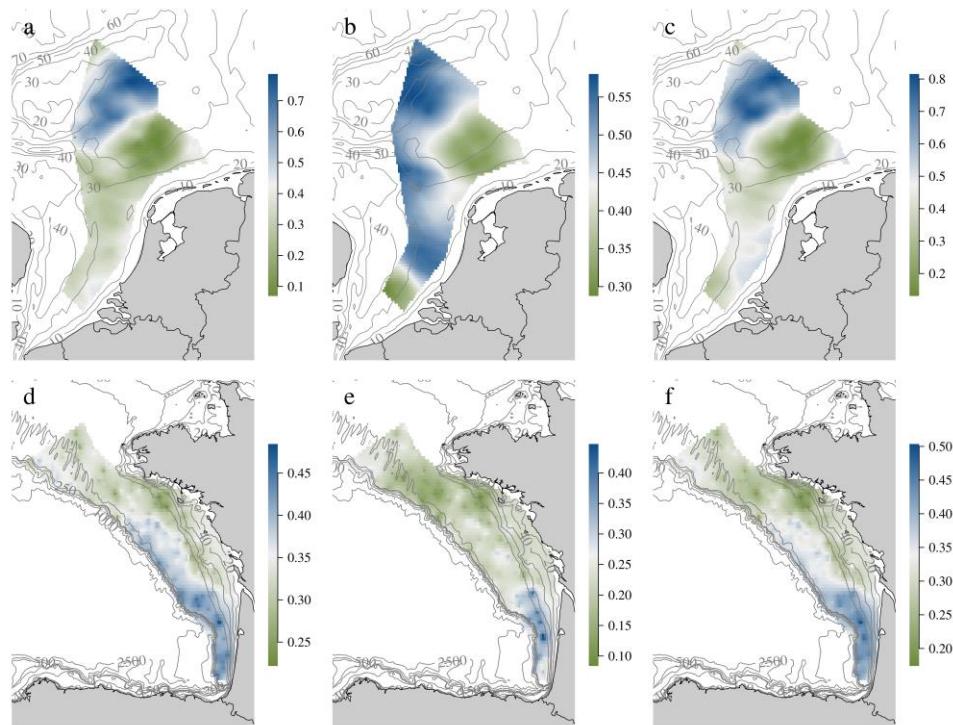
Fig. 7. Interpolation maps of the most responsive variables for (a–c) Dutch EEZ, (d–f) Bay of Biscay. (a,d) Sensitivity (SE), (b,e) recoverability (RE) and (c,f) vulnerability (SE + RE). Values are organism densities multiplied by trait scores, rescaled to the interval [0−1]

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, Tiano 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 (Lindegarth 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.

LITERATURE CITED

Baretta JW, Ebenhöh W, Ruardij 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/1012770/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, Wilsond 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 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
Abludomelita obtusata	1	2	3	1	1	1	1	1	1	51,162,230,521
Abra alba	2	3	2	2	1	2	3	4	1	124,129,290
Abra nitida	2	3	3	2	1	2	3	4	1	60,129,523
Abra prismatica	2	3	3	2	2	2	3	4	1	124,129,159,320
Abra tenuis	2	3	3	2	1	2	3	3	1	129,134,249,290
Acanthocardia sp.	3	1	3	2	2	4	3	4	1	129,190,319,386
Acrocnida brachiata	5	3	2	2	3	3	3	3	1	53,54,179,316,319,320
Acteon tornatilis	2	1	2	2	2	2	3	4	1	129,186,541,542
Actinauge sp.	3	1	3	4	3	4	3	3	2	337
Aequipecten opercularis	3	1	4	1	2	3	3	4	2	55,57,320,396
Alcyonium digitatum	5	2	4	4	3	4	3	3	2	227,228,244,339,468
Alcyonium glomeratum	5	2	4	4	3	4	3	3	2	193,227,228,244,339,468,478,479
Alitta virens	5	3	1	1	2	2	3	3	1	179,278,375
Alpheus glaber	3	2	4	1	1	2	2	2	2	271,350,385,390,420
Ampelisca brevicornis	2	2	3	1	1	2	1	1	1	105,122,320
Ampelisca diadema	1	2	3	1	1	1	1	1	1	105,190,266,319,322,355
Ampelisca macrocephala	2	2	3	1	1	2	1	1	1	266,322
Ampelisca spinipes	2	2	3	1	1	2	1	1	1	266,319,322,417,428,537
Ampelisca tenuicornis	1	2	3	1	1	2	1	1	1	322,455,489,509
Ampharete sp.	3	3	2	3	1	1	3	3	1	125,199,319,322,402
Amphipholis squamata	3	3	4	2	2	2	1	1	1	155,263,322
Amphiura chiajei	5	3	2	2	3	4	3	3	1	240,351
Amphiura filiformis	5	3	3	2	3	4	3	4	1	52,62,352,509
Anseropoda placenta	4	2	3	2	2	3	3	3	2	230,337
Antedon sp.	5	3	4	1	2	2	3	3	2	26,141,230,282,285,286,303,325,358
Antedon petasus	5	3	4	1	2	2	3	3	2	26,141,230,282,285,286,303,325,358
Aonides paucibranchiata	2	3	3	2	1	1	3	3	1	170,190,319,320,530
Aphelochaeta marioni	3	3	3	2	2	3	3	3	1	125,167,202,203
Aphrodita sp.	4	2	3	2	2	3	3	4	1	75,179,190,319,522
Aphrodita aculeata	4	2	3	2	2	3	3	4	2	75,179,190,319,522
Aporrhais pespelecani	3	1	4	2	2	3	3	3	1,2	129,297,322,388
Aporrhais serresianus	3	1	4	2	2	3	3	3	2	129,297,322,388
Arcopagia crassa	3	1	2	2	2	3	3	4	1	129,190,488
Arctica islandica	4	1	3	4	3	4	3	4	1	69,129,348,416,487
Aristaeomorpha foliacea	4	1	4	1	2	3	3	3	2	112,172,230,378
Armina loveni	2	2	3	2	1	1	3	3	2	160
Asbjornsenia pygmaea	1	1	3	2	2	3	3	4	1	129,190,319
Astarte montagui	2	1	4	2	2	3	3	3	1	129,430,450
Astarte sulcata	2	1	4	2	2	3	3	3	2	129,430,450
Asterias sp.	5	2	4	2	2	3	3	3	1	50,179,512
Asterias rubens	4	2	4	2	2	3	3	3	2	50,179,512
Astropecten sp.	3	2	3	2	2	3	3	3	1	179,185,209,322
Astropecten irregularis	4	2	3	2	2	3	3	3	2	179,185,209,322
Atelecyclus sp.	3	2	3	2	2	3	2	1	2	230,337
Atelecyclus rotundatus	3	2	3	2	2	3	2	1	2	230,337
Atelecyclus undecimdentatus	3	2	3	2	2	3	2	1	2	230,337
Atlantopandalus propinqvus	4	2	4	1	2	3	2	1	2	230,337
Atrina pectinata	5	1	4	4	2	3	3	4	2	89,401,405,427,544
Balanus crenatus	2	1	4	4	1	2	2	3	1	27,404,407
Bathyporeia elegans	1	2	3	1	1	1	1	2	1	176,177,243,322,361
Bathyporeia gracilis	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
Bathyporeia guilliamsoniana	1	2	3	1	1	1	1	2	1	114,176,177,243,361
Bathyporeia pelagica	1	2	3	1	1	1	1	2	1	114,176,177,361
Bathyporeia sarsi	1	2	3	1	1	1	1	1	1	114,190,361,510
Bathyporeia tenuipes	1	2	3	1	1	1	1	2	1	114,177,239,319,361
Bela nebula	2	1	3	2	1	2	3	3	1	129,135
Bodotria arenosa	1	2	3	1	1	1	1	2	1	261,264,322,454,539
Bodotria scorpioides	1	2	3	1	1	1	1	2	1	261,264,319,322,454,539
Branchiostoma lanceolatum	3	2	3	1	2	3	3	3	1	36,139,238,293
Brissopsis lyrifera	3	3	3	2	3	3	3	4	1,2	64,173,230,239
Buccinum humphreysianum	3	1	4	2	3	4	3	3	2	66,129,251,252,253,269,270,323,343
Buccinum undatum	3	1	4	2	3	4	3	3	1,2	129,269,270,323
Bylgides sarsi	2	3	3	2	2	2	3	3	1	3,322,438
Calliactis parasitica	3	1	4	4	3	4	3	3	2	179,230,337
Callianassa sp.	3	3	1	2	2	2	2	1	1	243,280,423,424
Calliostoma granulatum	3	1	4	2	2	3	3	3	2	179,230,337
Calocaris macandreae	3	2	1	1	2	3	3	2	2	61,230,356
Cancer bellianus	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
Cancer pagurus	5	1	1	2	3	4	2	1	2	34,40,179,322,535
Capitella capitata	3	3	3	3	1	1	2	3	1	4,46,243,336
Carcinus maenas	3	3	3	2	2	3	2	1	1	35,179,322,342
Caryophyllia sp.	2	3	4	4	2	4	3	3	2	179,230,337
Caryophyllia smithii	2	3	4	4	2	4	3	3	2	179,230,337
Chaetopterus variopedatus	5	3	1	3	1	2	3	3	1	149,156,230,485
Chaetozone setosa	2	3	2	2	1	2	3	3	1	88,230,237,243,319,376
Chamelea striatula	3	1	3	2	2	4	3	4	1	17,129,219,243,534
Cheirocratus sundevalli	2	2	3	1	1	1	1	1	1	105,261,319,484,521
Chlorotocus crassicornis	3	2	4	1	2	3	2	1	2	337
Cidaris cidaris	3	3	4	2	3	4	3	4	2	337
Colus gracilis	3	1	4	2	3	4	3	3	2	230,337
Colus islandicus	3	1	4	2	3	4	3	3	2	230,337
Corbula gibba	2	2	3	2	2	2	3	4	1	129,247
Corophium sp.	1	2	2	1	1	1	1	2	1	180,322,334
Corystes cassivelaunus	3	3	3	2	2	3	2	1	1,2	179,226,255,319,322
Crangon allmanni	3	2	3	1	2	2	2	1	2	9,44,230
Crangon crangon	3	2	3	1	2	3	2	1	1,2	108,179,232,397
Diastylis bradyi	1	2	3	1	1	1	1	1	1	138,243,264,322,508
Diastylis lucifera	1	2	3	1	1	1	1	1	1	102,380,389
Diastylis rathkei	1	2	3	1	1	1	1	1	1	389,508
Dichelopandalus bonnieri	3	2	4	1	2	3	2	1	2	230,337
Diogenes pugilator	2	1	3	2	1	1	2	2	1	309,317,318,490
Donax vittatus	2	1	2	2	2	2	3	4	1	19,129
Doris pseudoargus	3	2	4	2	1	1	3	3	2	129,230,486
Dosinia exoleta	3	1	2	2	2	4	3	4	1	129,190,496,499
Dosinia lupinus	3	1	2	2	2	4	3	3	1	129,190,497
Dyopedos monacantha	1	2	4	1	1	1	1	2	1	322,483
Ebalia sp.	2	3	4	2	1	2	2	2	1	230,295,319,445,446
Ebalia granulosa	2	3	4	2	1	2	2	3	2	230,295,319,445,446
Ebalia tuberosa	2	3	4	2	1	2	2	3	2	230,295,319,445,446
Echinocardium sp.	3	3	2	2	3	4	3	3	1	63,81,243
Echinocardium cordatum	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
Echinocardium pennatifidum	3	3	2	2	3	4	3	3	2	63,81,243
Echinocyamus pusillus	2	3	3	2	2	2	3	3	1	198,243,304,319,322
Echinus sp.	4	3	4	2	2	4	3	3	2	95,151,165,179,183,230,344
Echinus esculentus	3	3	4	2	2	4	3	3	2	95,151,165,179,183,230,344
Echinus melo	4	3	4	2	2	4	3	3	2	95,151,165,179,183,230,344
Ensis ensis	4	3	2	2	3	4	3	4	1	129,233,319
Ensis leei	4	3	2	2	2	3	3	4	1	129,305,319
Ensis magnus	4	3	2	2	3	4	3	4	1	115,129,179,236
Ensis siliqua	4	3	2	2	3	4	3	4	1	116,129,164,233
Eteone flava	3	2	3	2	1	1	3	3	1	111,230,284,319,376
Eteone longa	3	2	3	2	1	1	3	3	1	230,243,409,410
Eulalia sp.	3	2	4	2	1	3	3	3	1	154,190,230,319,322,371
Eumida sanguinea	2	2	3	2	1	2	3	4	1	65,243,319,322
Eunereis longissima	4	3	4	2	1	1	3	3	1	190,322,474
Eupolymnia nebulosa	4	3	3	3	2	3	3	3	1	37,38,211,212,320
Eurydice pulchra	1	2	3	1	2	2	1	1	1	181,230,262
Eusergestes arcticus	3	2	4	1	2	2	2	1	2	152,230,327
Euspira catena	3	1	4	2	2	3	3	3	1	18,129,298
Euspira fusca	3	1	4	2	2	3	3	3	2	18,129,273,298
Euspira nitida	2	1	4	2	2	3	3	3	1	129,273,298
Fabulina fabula	2	3	2	2	2	3	3	4	1	129,319,518
Funiculina quadrangularis	5	3	4	4	3	4	3	2	2	150,210
Galathowenia oculata	2	3	3	3	1	1	3	3	1	174,274,333
Gammaropsis sp.	1	2	4	1	1	2	1	2	1	257,319,322,354
Gammarus sp.	1	2	4	1	1	2	1	1	1	15,103
Gari fervensis	3	1	3	2	2	3	3	3	1	129,131
Gastrosaccus spinifer	2	2	3	1	1	2	1	1	1	42,179,313,319,410
Gattyana cirrhosa	2	2	1	2	2	3	3	3	1	111,243
Gilvossius tyrrhenus	3	3	1	2	2	2	2	1	1	148,322,383,480,481
Glycera sp.	5	2	1	1	3	3	3	3	1	73,106,107,319,322,366,533
Glycymeris glycymeris	3	1	3	2	3	4	3	3	2	21,189,230,443
Gnathophausia sp.	3	1	4	1	2	2	1	1	2	335,527
Goneplax rhomboides	3	1	2	2	2	3	2	2	2	230,337
Goniada maculata	3	2	3	1	1	2	3	3	1	190,243,274,319,320,329
Gracilechinus sp.	3	3	4	2	3	4	3	4	2	67,187,188,230,308,504,505
Gracilechinus acutus	3	3	4	2	3	4	3	4	2	188,230,308,505
Gracilechinus elegans	3	3	4	2	3	4	3	4	2	67,187,188,230,308,504,505
Harmothoe sp.	3	2	3	2	2	2	2	3	1	111,118,179,243,319,322,410
Harpinia antennaria	1	2	3	1	1	1	1	1	1	230,243,322,425,521
Haustorius arenarius	2	2	2	1	1	1	1	1	1	137,142,320,506
Hediste diversicolor	4	3	1	1	1	2	2	3	1	144,158,179,322,444
Henricia sp.	3	2	4	2	2	3	3	3	2	179,230,337
Heteromastus filiformis	4	3	1	3	2	2	3	3	1	41,182,453
Hiatella arctica	3	1	4	4	2	4	3	4	1	129,319,449
Homarus gammarus	5	1	1	2	3	4	2	1	2	30,246,359,456,513
Hyalinoecia tubicola	4	1	4	2	2	2	1	1	2	230,337
Hymenodiscus coronata	5	3	4	2	2	3	3	3	2	337
Hypereteone foliosa	3	2	2	2	1	2	3	3	1	319,322,376,532
Idotea linearis	2	2	4	1	1	2	1	1	1	179,184,230
Inachus sp.	3	2	4	2	2	2	2	1	2	224,225,294
Inachus dorsettensis	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
Inachus leptochirus	3	2	4	2	2	2	2	1	2	224,225,294
Inachus phalangium	3	2	4	2	2	2	2	1	2	224,225,294
Iphinoe trispinosa	1	2	3	1	1	1	1	2	1	101,322,454
Jassa marmorata	1	2	3	1	1	1	1	2	1	92,322,429,448
Jorunna tomentosa	3	2	4	2	1	1	2	3	2	179,230,337
Kellia suborbicularis	1	3	3	2	2	2	2	4	1	129,300
Kurtiella bidentata	1	3	3	2	2	2	2	3	1	129,230,365
Laetmonice sp.	2	2	3	2	2	3	3	3	2	230,337
Lagis koreni	3	2	2	3	2	2	3	4	1	125,243,360,482
Lamellaria perspicua	3	2	4	2	1	1	3	3	2	179,230,337
Lanice conchilega	4	3	2	3	1	2	3	3	1	179,199,243,278,319,406
Laonice sp.	4	3	1	3	1	2	3	3	1	47,319,322,458
Lepas sp.	3	1	4	4	1	1	2	3	2	28,206,230
Lepidonotus squamatus	3	2	4	2	1	3	3	4	1	322,398,410
Leptometra celtica	5	3	4	1	2	2	3	3	2	337
Leptosynapta inhaerens	5	3	2	2	2	3	1	1	1	179,319,322,451
Limecola balthica	2	2	3	2	2	3	3	3	1	129,213,287,307
Liocarcinus sp.	3	1	3	1	2	3	2	1	1,2	2,25,56,84,85,91,171,179,229,230,319,322
Liocarcinus depurator	3	1	3	1	1	3	2	1	2	56,171,179,229
Liocarcinus holsatus	3	1	4	1	1	3	2	1	2	2,84,85,91,230
Liocarcinus marmoreus	3	1	4	1	2	3	2	1	2	2,25,56,84,85,91,171,179,229,230,319,322
Liocarcinus pusillus	3	1	4	1	2	3	2	1	2	2,25,56,84,85,91,171,179,229,230,319,322
Liocarcinus vernalis	3	1	4	1	2	3	2	1	2	2,25,56,84,85,91,171,179,229,230,319,322
Lucinoma borealis	3	1	1	2	2	3	3	3	1	119,129,214,498
Luidia sp.	5	2	4	2	2	3	3	3	2	221,230,502
Luidia ciliaris	5	2	4	2	2	3	3	3	2	221,230,502
Luidia sarsii	5	2	4	2	2	3	3	3	2	221,230,502
Lumbrineris sp.	5	2	2	2	3	3	3	3	1	230,243,319,392,440
Lutraria lutraria	4	1	1	2	3	3	3	4	1	129,268
Macomangulus tenuis	2	3	3	2	2	3	3	4	1	20,29,129,133,190,472
Macropipus tuberculatus	5	1	3	1	2	2	2	1	2	216,230,357,367
Macropodia sp.	3	3	4	2	2	2	2	2	2	179,254,319
Macropodia rostrata	3	3	4	2	2	2	2	2	2	179,254,319
Macropodia tenuirostris	3	3	4	2	2	2	2	2	2	179,254,319
Mactra stultorum	3	3	2	2	2	3	3	4	1	82,129
Magelona filiformis	3	3	2	2	1	2	3	3	1	175,320,322,347,529
Magelona johnstoni	3	3	2	2	1	2	3	3	1	175,319,347,529
Magelona mirabilis	3	3	2	2	1	2	3	3	1	175,347,413,529
Magelona papillicornis	4	3	2	2	2	2	3	3	1	175,243,322,347,529
Maja brachydactyla	5	1	4	2	2	3	2	1	2	74,191,217,230
Maja squinado	5	1	4	2	2	3	2	1	2	217,230,292
Malacoceros fuliginosus	3	3	3	1	2	2	3	3	1	47,179,215,319
Malmgrenia lunulata	3	2	2	2	2	3	3	4	1	190,322,395,547
Marthasterias glacialis	5	2	4	2	2	3	3	3	2	33,179,230,291,387
Mediomastus fragilis	3	3	3	3	1	2	3	3	1	190,223,319,410,515
Megaluropus agilis	1	2	3	1	1	1	1	3	1	161,176,243,382,484
Mesopodopsis slabberi	2	2	4	1	1	1	1	1	1	136,179,400,520
Mimachlamys sp.	3	2	4	4	2	3	3	4	1	55,129,412,452
Modiolus sp.	4	1	4	4	3	4	3	4	1	129,130
Munida intermedia	4	1	2	2	2	3	2	2	2	208,230,296
Munida rugosa	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
Munida speciosa	4	1	3	2	2	2	2	2	2	86,230,394,435
Musculus sp.	2	2	4	4	2	3	2	3	1	129,310,338
Mya arenaria	4	1	1	4	3	4	3	4	1	58,59,129
Mya truncata	3	1	2	4	3	4	3	4	1	11,12,129,319
Mysia undata	3	3	2	2	2	2	3	4	1	129,190,328
Mytilus sp.	4	1	4	4	2	4	3	4	2	129,250
Mytilus edulis	3	1	4	4	2	4	3	4	1,2	129,250
Nassarius reticulatus	2	1	3	2	3	3	3	3	1	79,129
Natatolana borealis	2	1	2	1	2	2	1	1	1	260,265,314,477,484
Nephrops norvegicus	5	1	1	2	3	3	2	1	1,2	166,168,169,495
Nephtys 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
Notomastus latericeus	5	3	1	2	1	1	3	3	1	170,200,230,524,528
Nucula nitidosa	2	1	3	2	2	3	3	3	1	125,126,129,413,531
Nucula nucleus	2	1	2	2	2	3	3	3	1	129,319
Ocenebra erinaceus	3	1	4	2	2	2	3	2	2	179,324,460,466
Ophelia sp.	3	2	3	2	2	2	3	3	1	274,319,403
Ophiocomina nigra	4	3	4	2	3	4	3	3	2	179,230,337
Ophiothrix sp.	4	3	4	2	2	3	3	3	2	127,179,234,469,470
Ophiothrix fragilis	4	3	4	2	2	3	3	3	2	127,179
Ophiothrix luetkeni	4	3	4	2	2	2	3	3	2	127,179,234,469,470
Ophiura sp.	3	3	3	1	2	3	3	3	1,2	49,117,179,319,503
Ophiura albida	3	3	3	2	2	3	3	3	2	49,117,179,319
Ophiura ophiura	3	3	4	1	2	3	3	3	2	49,117,179,319,503
Orchomenella nana	1	2	4	1	1	1	1	2	1	346,484
Owenia fusiformis	3	3	2	3	2	2	3	3	1,2	13,125,179,196,322,362
Oxydromus flexuosus	3	3	3	1	2	2	3	3	1	220,381
Pagurus sp.	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus alatus	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus bernhardus	3	1	4	2	2	3	2	1	1,2	128,179,288,321
Pagurus carneus	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus cuanensis	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus excavatus	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus forbesii	2	1	4	2	2	2	2	1	2	128,179,275,276,288,321
Pagurus prideaux	3	2	4	2	2	2	2	1	2	128,179,275,276,288,321
Palaemon serratus	3	2	4	1	1	2	2	1	2	178,179,230,414
Palinurus elephas	5	1	1	1	3	4	2	1	2	207,242
Palinurus mauritanicus	5	1	1	1	3	4	2	1	2	207,242
Paraonis fulgens	3	2	2	2	1	1	3	3	1	157,319,410,418,536
Parapenaeus longirostris	3	1	4	1	2	2	3	2	2	241,272,461
Parastichopus regalis	5	1	4	2	3	3	3	3	2	337
Parastichopus tremulus	4	1	4	2	3	3	3	3	2	337
Paromola cuvieri	5	1	4	2	2	3	2	1	2	337
Pasiphaea multidentata	3	2	4	1	2	2	2	1	2	22,72,96,152,230,327
Pasiphaea sivado	3	2	4	1	2	2	2	1	2	72,96,230,327,526
Pasiphaea tarda	3	2	4	1	2	2	2	1	2	22,152,230,327
Pecten maximus	4	1	4	1	2	4	3	4	2	129
Pennatula phosphorea	4	2	4	4	3	4	3	3	2	230,337
Peringia ulvae	1	2	3	2	1	2	3	3	1	14,129,179,462
Perioculodes longimanus	1	2	1	1	1	1	1	1	1	31,243,484
Petricolaria pholadiformis	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
Phaxas pellucidus	3	3	3	2	2	3	3	3	1	129,299
Philine aperta	3	2	4	2	2	2	3	4	2	179,245
Philocheras echinulatus	2	2	3	1	1	1	2	1	2	230,283,368,369,391
Philocheras trispinosus	2	1	3	1	1	1	2	1	1	230,283,368,369,391
Pholoe minuta	1	2	3	2	3	3	3	3	1	87,231,322
Phoronis sp.	3	3	2	3	1	1	3	4	1	153
Photis longicaudata	1	2	3	1	1	1	1	3	1	261,345,353,484,525
Phyllodoce sp.	3	2	2	2	2	3	3	3	1	230,243,302,349
Pisidia longicornis	1	3	4	2	1	2	3	3	2	230,431,459
Pisione remota	3	2	3	2	2	2	3	4	1	146,319,320,471
Plesionika heterocarpus	3	2	4	1	2	3	2	1	2	6,7,94,97,192,241,289,315,377,379,408,434,46
Plesionika martia	3	2	4	1	2	2	2	1	2	241,315
Poecilochaetus serpens	3	3	3	3	1	1	3	3	1	132,170,190,319,322
Polybius henslowii	2	2	3	1	2	2	2	1	2	230,337
Polycheles typhlops	3	1	1	1	3	3	2	1	2	1,5,98,242,492
Polydora sp.	2	3	3	3	1	1	2	3	1	16,90,120,179,215,311,322,545
Pontocrates altamarinus	1	1	3	1	1	2	1	1	1	31,243
Pontocrates arcticus	1	1	3	1	1	1	1	1	1	31,32,320
Pontocrates arenarius	1	1	3	1	1	2	1	1	1	31,176,320,514
Pontophilus norvegicus	3	2	3	1	2	2	2	1	2	230,337
Pontophilus spinosus	3	2	3	1	2	2	2	1	2	230,337
Porania pulvillus	4	1	4	2	2	3	3	3	2	230,337
Portumnus latipes	3	3	2	1	1	2	2	1	1	100,230,301,501
Prionospio sp.	3	2	3	3	1	1	3	3	1	319,322,363
Processa sp.	2	2	3	1	1	2	2	1	2	230,337
Processa canaliculata	2	2	3	1	1	2	2	1	2	230,337
Processa nouveli	2	2	3	1	1	2	2	1	2	230,337
Psammechinus miliaris	3	3	4	2	2	3	3	4	1,2	50,179,230,267
Pseudocuma longicorne	1	2	3	1	1	1	1	2	1	101,319,322,454
Pteria hirundo	4	1	4	4	3	4	3	4	2	197,340,341,441,442,464,516
Pteroeides griseum	5	2	4	4	3	4	3	3	2	337
Pycnogonum litorale	2	1	4	2	2	3	1	3	2	23,179,256,491
Pygospio elegans	2	3	3	3	1	2	2	3	1	16,320
Rissoides desmaresti	3	2	1	1	2	2	2	1	2	235,242,511
Rostanga rubra	2	2	4	2	1	1	3	4	2	83,204,205,230
Scalibregma inflatum	3	2	1	2	1	1	3	3	1	45,143,170,312
Scaphander lignarius	3	2	4	2	2	2	3	4	2	230,337
Schistomysis sp.	2	2	4	1	1	1	1	1	1	230,319,330,400,432,433
Scolelepis squamata	3	3	1	1	2	2	3	3	1	47,121,243,465,473
Scoletoma fragilis	5	2	2	2	3	3	3	3	1	230,376,507
Scoloplos armiger	3	3	2	2	2	2	3	3	1	77,201,243,279,447
Sergia robusta	3	2	4	1	2	3	2	1	2	337
Sigalion mathildae	3	2	1	2	3	3	3	3	1	179,199,243,333
Solenocera membranacea	3	2	3	2	1	1	2	2	2	337
Spatangus purpureus	4	3	3	2	3	3	3	4	2	179,230,337
Sphenia binghami	2	3	4	4	3	4	3	4	1	129,222,319,540
Spio decoratus	2	3	3	3	1	1	2	3	1	123,199,218,230
Spio filicornis	2	3	3	3	1	1	2	2	1	243,467,475
Spio martinensis	2	3	3	3	1	1	2	3	1	123,215,230,319,475
Spiophanes bombyx	3	3	3	3	1	2	3	3	1	47,113,243,413
Spirobranchus triqueter	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
Spisula elliptica	2	1	3	2	2	3	3	4	1	129,190,319
Spisula solida	3	1	3	2	3	4	3	4	1	129,163,179,259
Spisula subtruncata	2	1	3	2	2	3	3	4	1	68,125,129
Stichastrella rosea	3	2	4	2	2	3	3	3	2	230,337
Streblospio shrubsolii	2	2	3	3	1	1	1	2	1	76,230,277,436
Streptosyllis websteri	1	2	3	2	3	3	3	3	1	194,230,333
Synchelidium maculatum	1	2	3	1	1	1	1	1	1	31,484,514,543
Tellimya ferruginosa	1	3	2	2	1	2	2	4	1	129,230,300,370
Terebellides stroemii	2	3	2	3	1	2	3	3	1	111,145,170,384
Tethyaster subinermis	5	2	4	2	3	4	3	3	2	337
Tharyx sp.	2	3	3	2	2	2	3	3	1	48,125,167,203,393
Thelepus cincinnatus	4	2	3	3	1	1	2	3	1	190,258,332
Thracia convexa	3	3	2	2	2	3	2	3	1	10,80,129,319,437
Thracia phaseolina	2	3	1	2	2	4	2	3	1	10,129,319,437
Thracia pubescens	3	3	2	2	2	4	2	3	1	10,129,319,364,437
Thyasira flexuosa	1	1	2	2	2	2	3	3	1	43,125,129,306
Turritella communis	3	1	3	2	2	3	3	4	1,2	129,297,322
Upogebia deltaura	3	3	1	2	2	3	2	1	1	319,322,500,519
Urothoe brevicornis	1	2	2	1	1	2	1	1	1	65,99,132,243,319
Urothoe marina	1	2	2	1	1	2	1	1	1	65,99,132,179,319
Urothoe poseidonis	1	2	2	1	1	2	1	1	1	65,99,132,179,243,319
Venerupis corrugata	3	1	2	4	2	3	3	4	1	129
Venus sp.	3	1	3	2	3	4	3	4	1	24,129,178,399
Venus casina	2	1	3	2	2	3	3	4	2	24,129,178,399
Westwoodilla caecula	1	2	3	1	1	1	1	1	1	32,320
Xylophaga dorsalis	2	1	3	3	1	1	3	4	2	109,110,195,422

REFERENCES

1. Abelló P., Cartes J.E., 1992. Population characteristics of the deep-sea lobsters Polycheles typhlops and Stereomastis sculpta (Decapoda: Polychelidae) in a bathyal mud community of the Mediterranean Sea. Marine Biology 114:109–117.
2. 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.
3. 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.
4. Adkins M., Schulze A., 2011. Development of Capitella sp. G from Galveston Bay, Texas. Marine Biology Research 7:202–207.
5. Aguzzi J., Bahamon N., 2009. Modeled day–night biases in decapod assessment by bottom trawling survey. Fisheries Research 100:274–280.
6. Ahamed F., Ohtomi J., 2011. Reproductive biology of the pandalid shrimp Plesionika izumiae (Decapoda: Caridea). Journal of Crustacean Biology 31:441–449.
7. Ahamed F., Ohtomi J., 2012. Growth patterns and longevity of the pandalid shrimp Plesionika izumiae (Decapoda: Caridea). Journal of Crustacean Biology 32:733–740.
8. 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.
9. 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.
10. Allen J.A., 1961. The British species of Thracia (Eulamellibranchia). Journal of the Marine Biological Association of the United Kingdom 41:723–735.
11. 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)? Helgoland Marine Research 57:132–138.
12. Amaro T., Duineveld G., Tyler P., 2005. Does Mya truncata reproduce at its southern distribution limit? Journal of Shellfish Research 24:25–28.
13. 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.
14. 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 packardi (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 Eupolymnia 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. Helgoland 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., Gutow 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 Mactra 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: Galatheidae). 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., Lòpez-Gonzàles 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 (Portumnus 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 triqueter 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. Reproductionof 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 Verhandelingen 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 Scolelepis 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 brevicomis (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'Ophiothrix 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., Thiébaut 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 Callianassa 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 Ría 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. Hydrobioiogia 426:97–103.

175. Fiege D., Licher F., Mackie A.S.Y., 2000. A partial review of the European Magelonidae (Annelida: Polychaeta): Magelona mirabilis redefined 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-Rodriguez 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 Parazoanth us 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 clypeasteriod Echinocyamus pusillus (0.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 feasability 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., Froglia 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, Brancyura). 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 (Linneaus) (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 Natatolana 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 Natatoluna borealis Lilj. 1851, a scavenging isopod from the continental slope of the Mediterranean. Deep-Sea Research I 44:2045–2067.

266. Kanneworff 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.) (Bivalia: Macteacea). 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). Smithonian 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) (Crangonidae: 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 Galatheidae. 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-pelicani (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. Lönning 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. Luttikhuizen P.C., Honkoop P.J.C., Drent J., 2011. Intraspecifc 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 péracarides 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 natatoire chez i'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., Garcia-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 Ocenebra 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 Corophiurn 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 Alcyonium 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., HartnollR.GH., 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 (Phyllodoce mucosa & Phyllodoce 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 Amphiura 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 Amphiura 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. Observationson the burrows and burrowing behaviour of Calocaris macandreae (Crustacea: Decapoda: Thalassinoidea). 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., Kanneworff 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: Phyllodocidae) 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 Aristaemorpha 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 rutllanti (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 Mclntosh 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., Sänger 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. Plyuscheva M., Martin D., Britayev T., 2004. Population ecology of two sympatric polychaetes, Lepidonotus squamatus and Harmothoe imbricata (Polychaeta, Polynoidae), in the White Sea. Invertebrate Zoology 1:65–73.

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 I'annélide Nephtys cirrosa (Ehlers 1868) en Manche Orientale et en Mer du Nord Occidentale. PhD thesis, Unversité 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. Lanice 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'Haploops nirae. Thèse de doctorat, université Pierre et Marie Currie, Paris, France, 320 p.

418. Risk M.J., Tunnicli 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 rutllanti. 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 Bahia 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 Bahia 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 Ligurean Sea (Mesiterranean, 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. Sheader 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). Helgoland Marine Research 69:249–258.
461. Sobrino I., Silva C., Sbrana M., Kapiris 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. Sriknshnadhas 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. Stancyk S.E., 1974. Life-history patterns of three estuarine brittlestars (Ophiuroidea) at Cedar Key, Florida. PhD thesis, University of Florida, 74 p.
470. Stancyk S.E., Shaffer P.L., 1977. The salinity tolerance of Ophiothrix angulata (Say) (Echinodermata: Ophiuroidea) in latititudinally 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., Elner 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 Natatolana 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 coralAlcyonium 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 tyrrhena (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 tyrrhena: a comparison of three different biometrical approaches. Marine Biology 127:435–442.
482. Thiébaut 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 (Dyopedos 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. Thorarinsdottir 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 Polycheles 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, Portumnus 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. VIIth 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. Węsławski 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., Olsgard 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 Gnathophausia Iongispina (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 Eutrophicationa 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 ($R^2_{adj.} = 0.65$) and trawling intensity ($R^2_{adj.} = 0.47$). Figure S2.1 displays the relationships between the raw data (trawling and abiotic data *ln*-transformed).
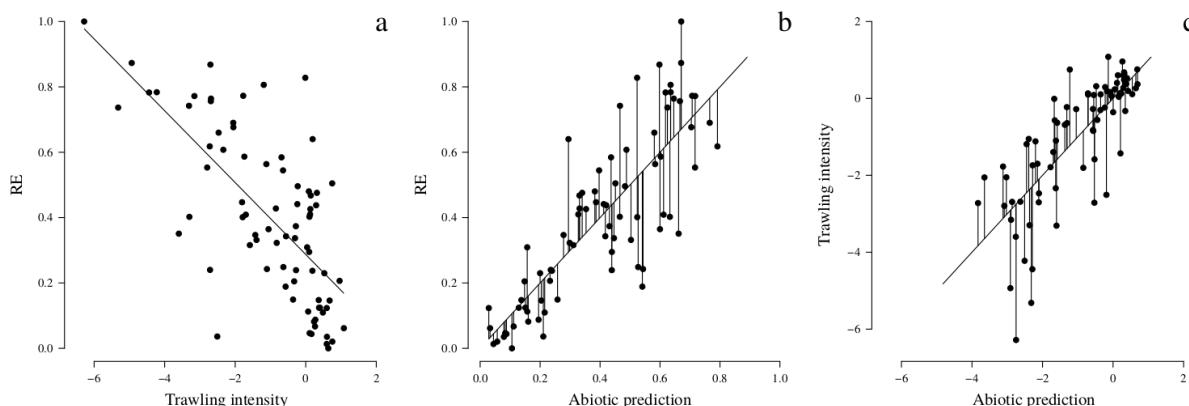
Fig. S2.1. Relationships between recoverability (RE, based on absolute taxon density), trawling intensity and abiotic variables. In b and c, abiotic prediction is the predicted value from the multiple regression of RE (b) and trawling intensity (c) on abiotic descriptors; vertical segments represent 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 $R^2_{adj.} = 0.02$. 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.
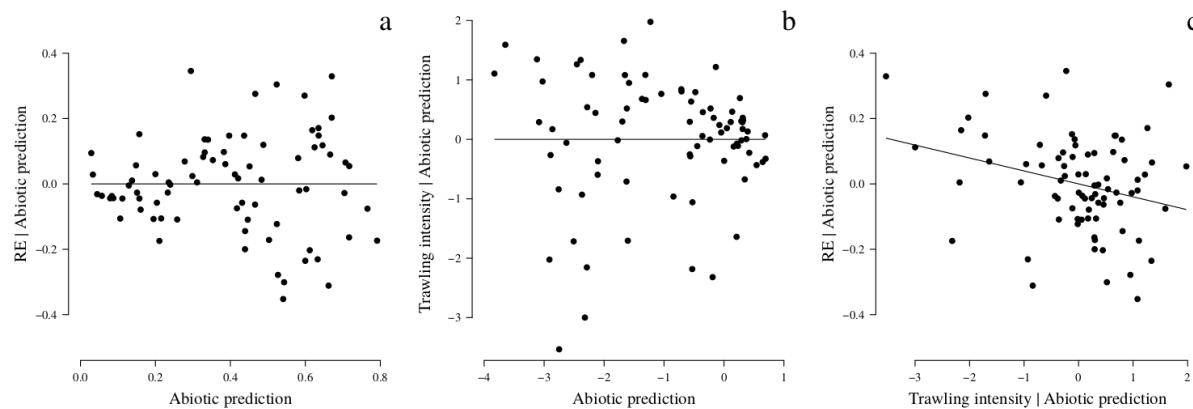
Fig. S2.2. a and b) Relationships between residual values from Figures S2.1b and S2.1c and abiotic prediction (the symbol "|" means "when controlling for"). These two sets of residuals are used in (c) to assess the response of RE to trawling intensity in the absence of abiotic interference (i.e. organism 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
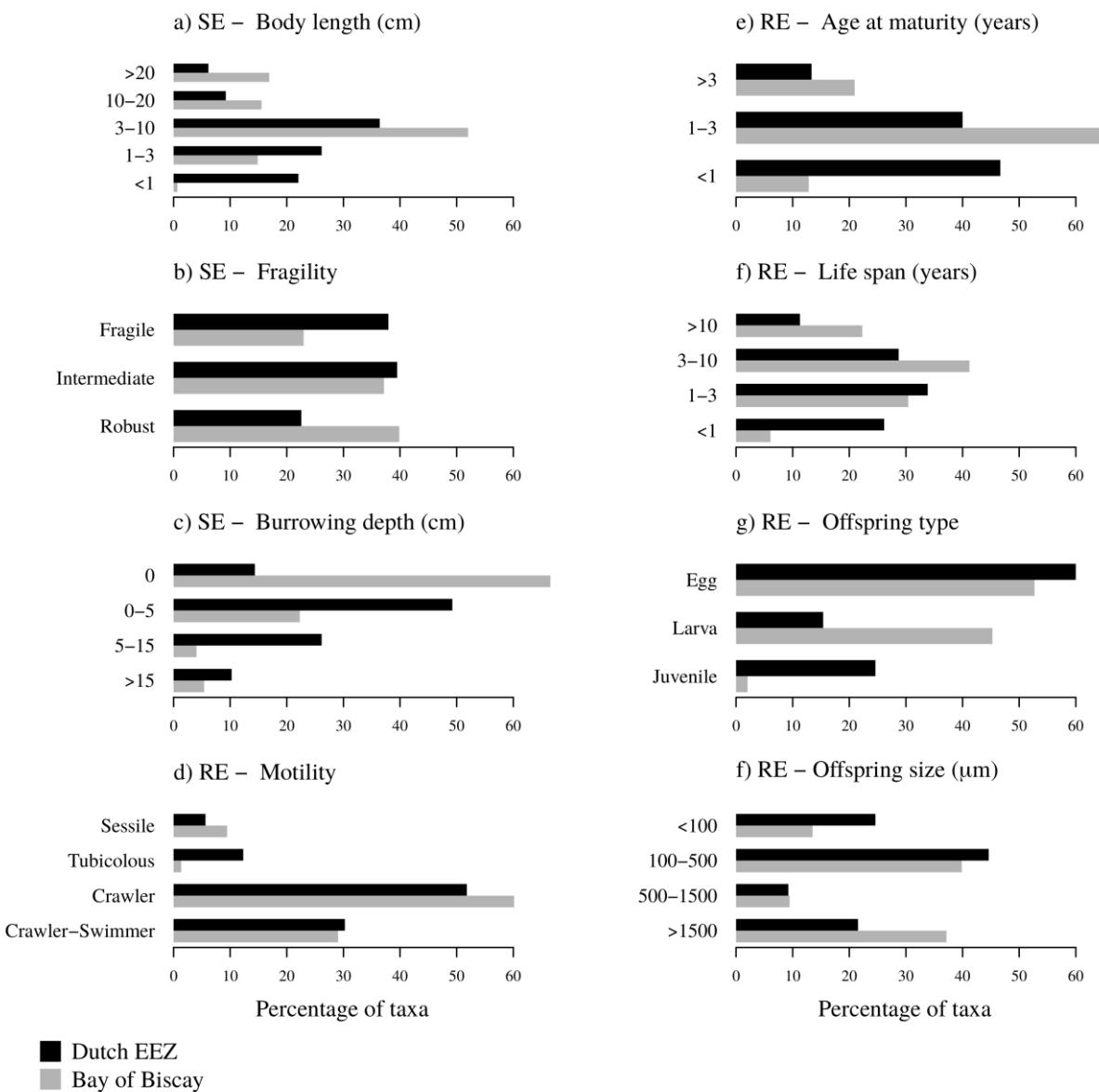
Fig. S3.1. Proportions of taxa for each biological trait modality in each of the two faunas.

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 *r*
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
		RE	0.19	0.13	0.23	0.10	0.09	0.04	−0.25
	Vulnerability	SE+RE	0.26	0.12	0.28	0.16	0.10	ns	ns
		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	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. ∩ Trawl.	Trawl. | Abio.	Partial *r*
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
		RM×OT×OS	0.67	0.30	0.67	0.37	0.30	ns	ns
		RE	0.65	0.47	0.67	0.20	0.45	0.02	−0.28
	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
		RM×OT×OS	0.13	0.08	0.25	0.17	0.00	0.12	−0.39
		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. ∩ Trawl.	Trawl. | Abio.	Partial *r*
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
		RM×OT×OS	0.60	0.23	0.61	0.38	0.22	ns	ns
		RE	0.64	0.28	0.65	0.37	0.27	0.02	−0.23
	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
		RM×OT×OS	0.35	0.17	0.34	0.17	0.17	ns	ns
		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 *r*
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
		RM×OT×OS	0.15	0.10	0.23	0.13	0.02	0.08	−0.38
		RE	0.17	0.10	0.25	0.15	0.02	0.08	−0.39
	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
		RM×OT×OS	0.14	0.14	0.26	0.12	0.02	0.12	−0.41
		RE	0.10	0.10	0.19	0.09	0.01	0.10	−0.36
	Vulnerability	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 r
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
		RE	0.06	0.10	0.15	0.06	ns	0.09	−0.35
	Vulnerability	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
		RE	0.14	0.05	0.17	0.13	0.02	0.03	−0.26
	Vulnerability	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 r
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
		RM×OT×OS	0.18	0.13	0.27	0.14	0.04	0.09	−0.40
		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
		RM×OT×OS	0.15	0.15	0.25	0.10	0.05	0.10	−0.40
		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 × 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.
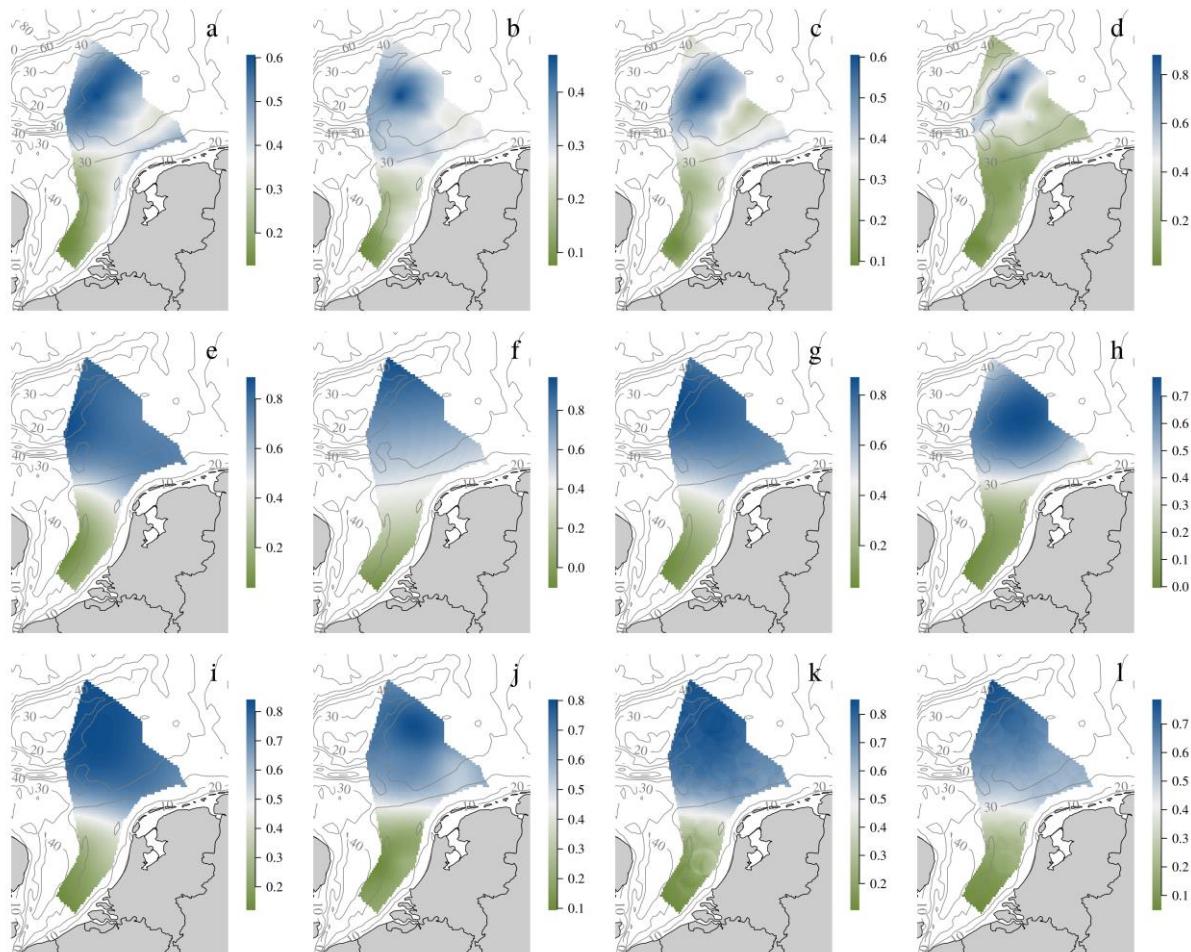
Figure S6.2. Interpolated relative organism densities in the Dutch EEZ. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE × RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.
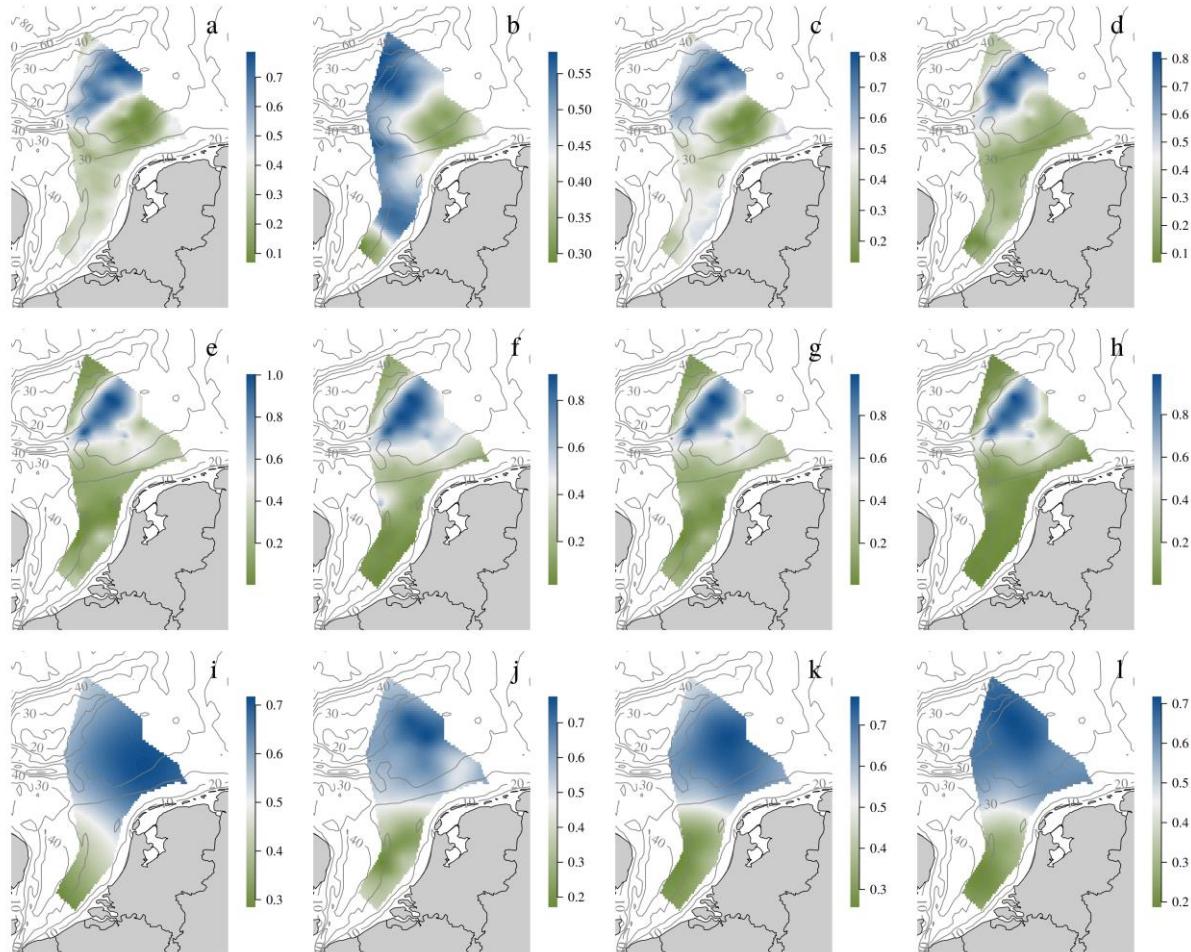
Figure S6.3. Interpolated absolute organism densities in the Bay of Biscay. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE × RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.
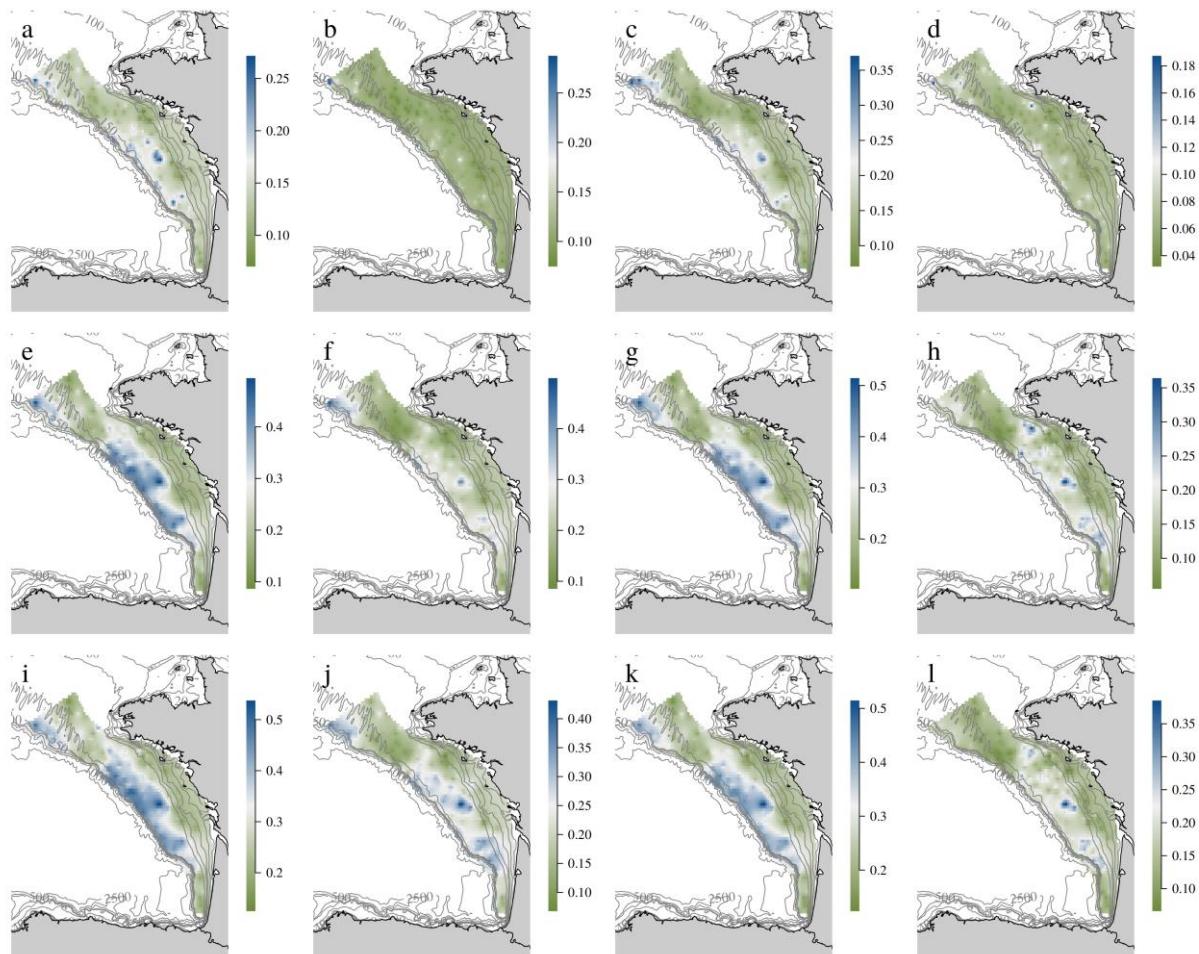
Figure S6.4. Interpolated relative organism densities in the Bay of Biscay. From left to right, sensitivity (SE; a, e and i), recoverability (RE; b, f and j), vulnerability SE + RE (c, g and k) and vulnerability SE × RE (d, h and l). From top to bottom, biomass, number of individuals and number of taxa. Values are multiplications of organism densities by standardised scores. High values express either high sensitivity, slow recovery or high vulnerability.