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Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions

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ABSTRACT

The physical impact of bottom towed fishing gears does not only reduce the abundance and biomass of species, but also alter the overall species composition and, through this, the functioning of benthic communities. The vulnerability of a species is determined by its individual combination of morphological, behavioural and life history traits. In turn, ecosystem functions are most affected when those species identified as vulnerable, contribute disproportionately to that function. On the basis of this paradigm, trait-based indices of physical resistance (**RI**) and recovery potential (**RPI**) were developed and combined into an overall vulnerability index on a species level, the **RRI** or **R**esistance and **R**ecovery **P**otential **I**ndex. The developed indices can be used to explore how resistance and recovery potential of benthic communities change over different levels of trawling. Furthermore, the **RRI** allows for dividing the benthic community into groups expressing different levels of vulnerability that can be linked to ecosystem functions to explore functional vulnerability to trawling. The **RRI** index futher opens up the possibility for scenario modelling by simulating the extinction or loss of vulnerable species and its effects on functions. This may be of particular interest in data poor case studies that lack trawling gradient data, or to explore the consequences of potential increases in fishing effort. The validity of the trait-based **RRI** index was tested by comparing individual species' **RRI** scores to empirically observed responses over a trawling gradient. **RRI** score and observed responses (regression slopes) were significantly correlated providing support for the rationality of the approach. Moreover, further analysis of the data evidenced clear increases of resistance and resilience indices over the trawling gradient, demonstrating that communities lost vulnerable species with increasing trawling. When exploring the effects of trawling on the bioturbation, as a chosen ecosystem function, we found it to be disproportionately affected though the loss of vulnerable species. The proposed indices provide new insights into the link of species vulnerability and function. Such information is of vital interest to environmental managers focused on preserving ecosystem functions and services in the face of anthropogenic global change.

1. Introduction

Globally, fishing impacts represent one of the main anthropogenic pressures acting on the marine environment (Clark et al., 2016; Eigaard et al., 2017) with negative consequences for the productivity and functioning of locally affected benthic ecosystems (Hiddink et al., 2011; Olsgard et al., 2008; Queirós et al., 2006). To safeguard the integrity of benthic ecosystems from fishing related impacts, various policy initiatives (e.g. among others Magnuson Stevenson Act USA, European Marine Strategy Framework Directive EU) have been promoted within the context of an ecosystem-based approach to fisheries management (Berg et al., 2015; Biedron and Knuth, 2016; Garcia et al., 2003). However, to evaluate the effectiveness of regulatory interventions, it is essential to monitor the health or status of benthic habitats through indicators that are able to capture changes in the structure and functioning of benthic ecosystems (de Juan et al., 2015; Rice et al., 2012).

Indicators that measure the status of benthic habitats have primarily been based on community metrics such as density, biomass and diversity (Hiddink et al., 2020) of the entire or of a specific size fraction of the benthos (McLaverty et al., 2020). A recent meta-analysis by Hiddink et al. (2020) concluded that community biomass as an indicator of fishing impacts gave the most reliable and consistent responses

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compared to other community indicators. The disadvantage of these generalized community indicators is that, on their own, they cannot provide estimates of the functional status or loss associated with fishing impacts, as biomass and functioning may be reduced at different rates (Thrush et al., 2006). Thus, which functions are most affected by trawling and to which degree will be defined by the biomass composition of species, their contribution towards a function and, most importantly, their vulnerability to trawling. The vulnerability of a species will in turn depend on the morphology, behaviour and life history characteristics of the species (Bremner et al., 2006; de Juan et al., 2020, 2007; Kenny et al., 2018). Therefore, an ecosystem function will be most affected by a particular human activity if the species that exhibit this function are also highly vulnerable to this activity.

To be able to describe and assess functional ecosystem changes in marine communities, benthic ecologists have implemented the concept of biological traits (Bremner et al., 2003; Bolam et al., 2014; Törnroos et al., 2019). Hereby, species' biological attributes that describe certain aspects of their morphology and behaviour are used with the aim to approximate the ecological role of the species (Bremner et al., 2003; Törnroos and Bonsdorff, 2012). Simple examples are categorisations into morphological attributes such as size or fragility (Shin et al., 2005), while others are related to behaviour, for example mobility and feeding mode (Smale, 2008), and to life history traits, such as maximum size, fecundity or similar (King and McFarlane, 2003).

Thus far, the majority of trait-based studies investigate the effect of anthropogenic stressors at a community level, aiming to gain insights into how they change the traits, or rather the functional (trait) composition of a community. Within this approach, traits are weighted by the abundance or biomass of all species exhibiting the selected trait (Bremner et al., 2003) and this pooled data is subsequently related to a stressor such as trawling (Villéger et al., 2010; Hiddink et al., 2019). The challenge with this approach is that the observed trait responses cannot indisputably be linked to the stressor nor can the results of such studies be easily generalized. This stems from the fact that the individually analysed traits are in fact the result of a combination of interdependent traits exhibited by the species. Some of the traits expressed by a species may facilitate a certain response to a stressor, while others may impede it. Thus, it might be the interplay, or sum of opposing, additive or synergistic traits, that will determine the response of a species to a stressor. As an example, species living on the surface of the seabed are likely to be impacted by trawling (Tiano et al., 2020); however, if surface dwelling species have a highly resistant shell and have a large reproductive potential, they may survive trawling impacts and quickly compensate for individual losses at a population level (Bremner et al., 2005). If we had several species with a similar traits' combination dominating the community, it could be wrongly concluded that trawling had little or no effect on organisms that inhabit the seabed surface. While this may be true for the particular area analysed, other areas, with different species composition, may show different responses. Thus, analysing the responses of traits at a community level has the potential to introduce bias and lead to spurious and inconsistent conclusions about the impact of a stressor.

To overcome some of these shortcomings, it has been suggested to group species into vulnerability groups according to a set of traits that are a-priori linked to a stressor or ecological function (de Juan et al., 2009, 2014 Bolam et al., 2014). Within this paper, we introduce new trait-based indices for benthic species and link these to a well-defined ecosystem function, i.e., bioturbation. The indices are based on empirical knowledge on the link between the vulnerability of a species to trawling and specific morphological, life history as well as behavioural characteristics (Jørgensen et al., 2016). In general, large, fragile and slow reproducing species living on the surface of the seabed appear to be the most affected by chronic trawling; while robust, small and fast reproducing species tend to be the least affected (de Juan et al., 2012; Jennings and Kaiser, 1998a; Van Denderen et al., 2015). From this general observation, two subgroups of traits can be delineated: those related to the physical resistance potential of a species (i.e., traits related to body size, living habit, body form) and those related to its recovery potential (i.e., traits such as small body size and fast reproduction). Both of these trait groups contribute to the vulnerability (or the opposite resilience) of species to trawling.

The development of our indices followed the same logic and, therefore, we first constructed two sub-indiceses a) a physical "**R**esistance **I**ndex" (**RI**), considering morphological and behavioural aspects of the species (e.g., body structure or living position), and b) a "**R**ecovery **P**otential **I**ndex" (**RPI**), considering traits related to the reproductive strategies and population growth potential. These two indices were subsequently combined into an overarching index that we named "**R**esistance and **R**ecovery **P**otential **I**ndex" or **RRI**. This index can be used as a standalone index to attain a measure of the vulnerability or resilience of a community to trawling. Additionally, it can be used to explore the link between vulnerability and ecosystem functions. Besides introducing the RRI and its sub-indices, the present study aimed to validate and demonstrate the multiple uses of the index by applying it to benthic data from the North-Eastern Irish Sea *Nephrops* fishing ground (Hinz et al., 2009) and linking it to a well-established functional index, the benthic community bioturbation potential index (BPc) developed by Queirós et al. (2013).

2. Methods

Within this this section, we first describe the calculation of the indices based on traits information and their scoring, then, we outline the validation of these indices based on previously collected case study data from the Irish Sea (Hinz et al. 2009, see Section 2.2.). For the validation, we investigate the effectivity of the RRI to represent vulnerability to trawling by comparing index scores to observed responses to trawling at a species level. Furthermore, we describe the application of the RRI as a community level indicator of resilience/vulnerability. Finally, we portray how the vulnerability of species can be linked to an ecosystem function. As an example, we link the RRI to the benthic community Bioturbation Potential index (BPc) and show how it can be used within scenario simulations in data poor areas.

2.1. Formulation of indices

To determine the vulnerability of species to trawling, we developed two additive indices: the Resistance Index (RI) and the Recovery Potential Index (RPI). The combination of the two indices into a third index, Resistance and Recovery potential Index (RRI), aims to assess the potential vulnerability of a species. All three indices are designed as weighted directional indices, where the final calculated score of a species in the respective index reflects the contribution of all relevant traits combined towards the objective of the RRI index, that is expressing the resilience/vulnerability of species to trawling.

2.1.1. RI and RPI calculations

The rational for the RI and RPI indices follows from the objective to describe the physical resistance and the recovery potential of a species to trawling. For this, we created simple indices using readily available traits information, avoiding traits with known gaps. The traits related to resistance included: body form, body texture, size and environmental position. While traits related to the potential recovery after disturbance were related to reproduction and growth: size, adult longevity, reproductive frequency, development type, regeneration of body parts and scavenging as a feeding type (see Tables 1 and 2 for trait categories and their rational). The feeding type scavenger was included as trawling is known to significantly benefit species with this feeding mode (Groenewold and Fonds, 2000; Tillin et al., 2006) and it may thus increase survival and reproductive potential of these species. The trait body size was used in the two indices as size is related to the physical resistance of a species to trawling, with larger species having a higher tendency to be

Table 1
Traits and trait categories included in the calculation of the Resistance Index (RI). For each trait a description and a rational for the ranked scoring is provided. The balancing score is a multiplication factor to give each trait the same weight towards the final index.

Traits	Trait categories	Description	Rational	Scoring	Balancing score
Body form	Erect	All species that have a vertical body orientation and are therefore more prone to be caught, up-rooted or broken (includes tubes)	As the trawl gear is pulled over the seabed surface animals that protrude from the surface are more likely to be damaged or caught by the trawl gear. Flat and low-profile animals may therefore have a higher potential to survive the passage of a trawl	1	1.66
	Spherical (round body)	Animals with both similar vertical and horizontal depth		2	1.66
	Low profile (thin)	Species with low vertical body depth (flattened) or worm like		3	1.66
Body texture	Brittle	Species that break with modest physical impact	The body texture of an animals will determine its likelihood of being damaged by a physical disturbance. Brittle and unprotected species will have a higher potential to be damage compared to species with a durable sin or hard exoskeletons and shells. Furthermore, if caught by the trawl and discarded these organisms have a higher chance of survival due to their protective textures as they may be more resistant to physical handling on deck and desiccation	1	1.25
	Unprotected soft tissue	Species only showing soft tissue		2	1.25
	Thin exoskeleton or shell	Species with thin protective structure that only withstand low impact (includes tubes)		3	1.25
	Durable/ Flexible	Species that are rubbery or durable nature or are flexible (with stand moderate impact)		3	1.25
	Hard exoskeleton or shell	Species with hard shells able to withstand hard impact (includes tubes)		4	1.25
Size (mm)	>100	Estimated average size categories of animals (these may be different for different areas)	Larger animals are more likely to interact with the trawl gear compared to smaller animals. For example, while large animals may suffer direct damage when encountering the fishing gear smaller species may simply be displaced by the pressure wave or are able to pass through the net undamaged.	1	1
	51–100			2	1
	21–50			3	1
	11–20			4	1
	0–10			5	1
Living position	Epibenthic and Interface	Animals living directly above or on top of the sediment. Animals may be partially buried	The living position determines if the animal is likely to encounter the trawl gear. Animals on the surface or shallow buriers are thus more likely to get damaged or killed by trawling. Deep borrowing organisms are in contrast less likely to be damaged by the passing gear with the sediment providing protection from direct contact with the fishing gear.	1	1.66
	Middle	Animals fully buried generally below 1–5 cm below the surface		2	1.66
	Deep	Animals living below 5 cm depth within the sediment		3	1.66

Table 2
Traits and trait categories included in the calculation of the Recovery Potential Index (RPI). For each trait a description and a rational for the ranked scoring is provided. The balancing score is a multiplication factor to give each trait the same weight towards the final index.

Traits	Trait categories	Description	Rational	Scoring	Balancing score
Size (mm)	>100	Reported and estimated average size categories of benthic animals (these may be different for different areas)	Larger organisms tend to grow slower and populations therefore take longer to recover from trawling. In contrast smaller organisms tend to have faster growth and populations may therefore recover faster.	1	1
	51–100			2	1
	21–50			3	1
	11–20			4	1
	0–10			5	1
Adult longevity	>6yrs	Reported and estimated average length of adult life	Longer lived species may reach reproductive maturity later in life compared to short lived species. Recovery potential will therefore tend to be higher for short lived species compared to long lived species	1	1.25
	3–6yrs			2	1.25
	1–3yrs			3	1.25
	<1yr			4	1.25
Reproductive frequency	Semelparous-monotelic	Reproduces only once, then dies	The reproductive frequency is related to reproductive output. animals that only reproduce once during their life have lower recovery potential compared to species that produce serval times or continuously during their life time.	1	1.25
	Iteroparous-polytelic	Reproduces several (once-or twice) times during life time		2	1.25
	Semi-continuous	Reproduces semi-continuously throughout the year and life time		3	1.25
Developmental type	Benthic - direct	Direct benthic development	The larvae developmental type relates to the recovery potential from trawling through the paternal investment into larvae and the potential of trawling to damage nursery habitats. In general clutch size and paternal investment are higher in direct benthic development and lecithotrophic compared to planktonic or development through fission or fragmentation. Additionally, benthic direct development may be directly negatively affected by trawling though habitat disturbances. In contrast there may be some facilitation through trawling for species developing through fragmentation.	1	1.25
	Lecithotrophic	Development through a planktonic larval stage but is nourished by internal resources		2	1.25
	Planktotrophic	Development through a planktonic larval stage that feed as plankton		3	1.25
	Fragmentation/ Fission	Development through fragmentation of body parts or fission		4	1.25
Regeneration of colony or body parts	Y/N	If damaged individuals or colony can survive and regenerate to become a fully functional organism	Animals with regenerative capacities may be able to sustain a certain amount of damage and survive providing the potential for recovery due to reduced mortality.	5	1
Scavenging Feeding type	Y/N	Scavenging as a main feeding trait	Trawling is known to significantly benefit species with this feeding mode. Increased energy intake may lead to faster growth and higher reproductive output.	5	1

caught or damaged, and also to the potential to recover after trawling, as small organisms tend to have faster growth and reproductive cycles compared to large slower growing organisms with less frequent reproduction (Jennings and Kaiser, 1998b).Table 3

Following the methodology of biological trait analysis (Bremner et al., 2003; Törnroos & Bonsdorff, 2012), the traits are collected for each species and compiled in a matrix. Trait categories are then assigned to the selected traits; in our case study e.g. body texture had the following five categories: brittle, unprotected soft tissue, thin exoskeleton or shell, durable /flexible, hard exoskeleton or shell. Species are then scored for their affinity to that trait category following the fuzzy scoring method using a scale of 0 (no affinity) to 1 (high affinity), with a total score of 1 for each trait (Bremner et al., 2003). The fuzzy coding allowed the species to vary in the degree in which it exhibited affinity to a specific category within a trait. The traits' assignment was based on available literature, information from online databases (e.g., BIOTIC, www.marlin.ac.uk/biotic and others see Appendix S1) and experts' knowledge. When no information on a trait was available for a species, information for the genera was considered; a minor proportion of cases had family or higher group level information. All literature sources of trait information have been acknowledged, as well as the amount of expert knowledge used in populating the traits matrix(see S1).

To calculate the indices for a particular species, the fuzzy coding of traits as described above was multiplied by the directional weighting scores of the index. Scores were given on the logical proneness of a specific trait category to be impacted by trawling; e.g., in the case of "body form", to be caught, broken or uprooted by a passing trawl, i.e., they were ranked 1 to 3 respectively, with erect contributing least to resistance and species with a low vertical depth contributing the most. To ensure each trait category had the same influence on the final index, the trait category rank values were multiplied by the maximum number of trait categories in any one trait (which was 5) divided by the number of traits categories in the observed trait (Balancing Score see Tables 1 and 2). The contribution of each trait to the respective index was kept equal as there is uncertainty about the precise strength of influence of each individual trait towards the indices' objectives, i.e., resistance or recovery potential (for a summary of the directional weighting scores and its rational see Table 1 and 2).

To normalize both index scores, and thus providing results on a similar scale (0 to 1), the following formula was used:

$$Species\ normalized\ score = \frac{(\sum Trait\ category\ scores\ of\ a\ species - Min\ score)}{(Max\ score - Min\ score)}$$

Values close to 1 for the RI of a species indicates that it is potentially highly resistant to trawling, while a value of 1 for the RPI indicates high recovery potential due to the associated life history traits.

2.1.2. RRI calculations

To calculate the Resistance and Recovery Potential Index (RRI), the mean of both individual normalized index scores (RI and RPI) was calculated (from 0 = highly vulnerable, to 1 = highly resilient). The RRI species scores were subsequently categorised into five levels to identify species with similar scores for the subsequent analyses: 0.8–1 = Very High RRI, 0.6–0.79 = High RRI, 0.4–5.9 = Moderate RRI, 0.2–0.39 = Low RRI and 0–0.19 = Very Low RRI.

Table 3
Summary of trait categories and scores used to calculate BPc as described by Queirós et al (2013).

Mobility (Mi)	Score	Sediment reworking types (Ri)	Score
Organisms that live in fixed tubes	1	Epifauna	1
Organisms with indicates limited movement	2	Surficial modifier	2
Organisms with slow, free movement through the sediment matrix	3	Upward and downward conveyors	3
Organisms with free movement, that is, via burrow system	4	Biodiffusors	4
		Regenerators	5

2.2. Validation of the RRI index

2.2.1. The Irish Sea case study and its macrofauna data

To validate the developed indices, we used macrofauna data previously collected over an active fishing ground for Norway lobster (*Nephrops norvegicus*, Linnaeus) and gadoid fish in the north-eastern Irish Sea in 2007. This data was previously published by Hinz et al. (2009) to investigating the effects of chronic trawling on benthic communities. For more detailed information about the sampling design, as well as the fishing effort calculation, refer to Hinz et al. (2009). In short, macrofauna data was collected at 15 sites over a gradient of fishing intensity varying from 1.3 times trawled/year to 18.2 times trawled/year. Both benthic infauna (day grab samples 0.1 m^2) and epifauna (2-m beam trawl) were sampled and standardized to m^2 biomass. Physical parameters such as sediment type were kept constant to avoid any confounding habitat effects. The two datasets were combined into one single data matrix for the subsequent analyses (for benthic data see S2 and for trawling intensity and physical characteristics of sampling sites see S3). The methodology for calculating the two sub-indices and the final RRI index was applied to the macrofauna dataset.

2.2.2. Effectivity of the RRI to represent vulnerability to trawling on a species level

The effectivity of the indices to represent the overall vulnerability of species to trawling was validated by comparing the calculated RRI scores of individual species to observed responses of those same species over a gradient of trawling intensity (as recorded by Hinz et al., 2009), using linear regression slopes. Prior to analysis, the individual species biomass data was normalized. For the validation analysis, we considered only species that had sufficient data: occurred at least over 4 stations out of 15, i.e., over 30%. We expected that for our RRI index to be valid, there should be a significant correlation between the species RRI scores and the individual species regression coefficients from the observed data. The correlation between the RRI index and regression coefficients was calculated for species groups with different occurrences over the sampling stations. Through this we explored if the correlations would improve when using data of species that had successively higher occurrences over our sampling area. The assumption was that the responses of common species would contain less errors related to false zero observations (i.e., due to absence at sites unrelated to trawling) making the correlation between RRI score and coefficient more robust and representative for the validation of our index. However, considering that some of the less common species are also those highly vulnerable to trawling, we decided to present the results of all correlations above the aforementioned minimum threshold of 30% occurrence over the sampling stations (see above). Three species in the validation analysis form a commensal type of association with another larger species. The small bivalve *Tellimya ferruginosa* lives associated with irregular urchins such as *Echinocardium* spp, while the small bivalve *Kurtiella bidentata* and the polychaeta *Podarkeopsis helgolandicus* are associated with brittle stars such as *Amphiura* spp. In these cases, the lower scoring host species RRI was used and not the original score calculated based on the species traits. The assumption was that the hosts' response to trawling would have a greater influence on the response of the associated species than the calculated species own RRI score.

2.2.3. Modelled responses based on RRI grouping of species

We investigated the observed responses of species, when grouped according to their RRI index scores, to test expected species responses to trawling (i.e., Low RRI species showing a strongly negative trend, followed by a less negative response for species of the Medium RRI group and non or a positive response for High RRI species). RRI group responses were modelled on a species level using generalized mixed modelling (GLMM) on the observed case study data, using the RRI group category as random effect (i.e., a grouping factor). As above, we used normalized biomass data versus fishing effort to calculate the regression coefficients by species. The resulting model relationships are thus the mean responses of species belonging to a RRI group. For the analysis, we pooled species with very low and low RRI scores as the former group only contained two species. Species with very high RRI scores did not exist within our study area, and therefore we investigated the response of three RRI groups: Low, Moderate and High. These three groups were maintained for all subsequent analysis. Note that the RRI group High only contained three species. The GLMM models were tested for their significance following procedures outlined by Zuur et al. (2009).

2.2.4. Relationship of indices (RI, RPI, RRI) to trawling on a community level

The relationship between scores of the indices at a community level and trawling were explored by linear regression models. An average score of the respective index on a community level was calculated by multiplying species index scores by species biomass at a respective station, subsequently summing all individual scores of that station and dividing this sum by the total biomass of the respective station.

2.3. Linking vulnerability to function

2.3.1. Response of bioturbation potential (BPc) to trawling

The benthic community Bioturbation Potential index (BPc) introduced by Queirós et al. (2013) was selected to demonstrate the link between RRI and ecosystem functions.

BPc takes into account the average size and abundance of organisms attained from sample data and combines these with bioturbation weighting factors based on categorical scales describing the mobility and sediment reworking of an organism (Queirós et al 2012). The following formula describes the calculation of BPc of a benthic community:

$$BPc = \sum_{i=1}^{n} \sqrt{\frac{Bi}{Ai}} \times Ai \times Mi \times Ri$$

Bi and Ai are the biomass and abundance of species/taxon *i* in a sample. Mobility (Mi) ranges from 1 (living in a fixed tube) to 4 (free three-dimensional movement via burrow system). Sediment reworking (Ri) ranges from 1 (epifauna that bioturbates at the sediment–water interface) to 5 (regenerators that excavate holes, transferring sediment at depth to the surface). For the present paper, we used the trait information provided by Queirós et al. (2013) for 1033 macrofaunal species in the case study data by extracting the relevant information to match our species list. Most species were already included within the database. Only 7 species were not found in the database provided by Queirós et al. (2013) and information for these species was therefore added by the present study (see S4 for a full species list and their relevant biological traits categorisation) using published descriptions of species bioturbation behaviour or, in its absence, information on closely related species.

The relationship between trawling versus BPc for different RRI groups (i.e., low, medium, high) was investigated using linear regression models. At each station, the summed bioturbation potential was calculated for each group. To linearize the data, all regressions were performed after log transformation.

2.3.2. Scenario modelling of the effect of trawling on bioturbation

We undertook a stress test modelling, emulating a scenario where little benthic data is available but the potential consequences of species removal or reductions of abundance are to be explored. For the scenario modelling, the data from the least impacted site in the Irish Sea case study was used as the baseline. We modelled the effect on bioturbation potential from 1) directed elimination and 2) reductions in species abundances, based on the species' RRI ranking, which provided an indication of the species' vulnerability to trawling.

2.3.3. Directed extinction scenario of low and high RRI species

We simulated the complete extinction of the 5, 10, 20, 30 and 40 percent of the most vulnerable species based on their RRI ranking (low RRI scores). We contrasted this deletion of species with random deletions, i.e., removing species at random from the species list considering the same number of species as removed for the low RRI ranking species. Random removals were performed by the random subsampling function in R (sample, base v3.6.2) and repeated 999 times. The resulting "directed deletion" scenario can be compared to the position and slopes of the "random deletion". If the slope of the directed removal is found to be above the random slope, vulnerable species are not strongly linked to that function. In contrast, if the slope is found below the random deletion slope, there is a strong indication that some of the vulnerable species contribute disproportionality to the function analysed. If the slopes of random and directed deletion are similar, vulnerability and function are not linked.

Furthermore, we reversed the removal to assess the contribution of non-vulnerable species to trawling, i.e., species ranked with a high RRI score to the bioturbation potential. In this scenario, we removed 5, 10, 20, 30 and 40 percent of the most resistant and resilient species from the species list and subsequently calculated the BPc. All scenario responses were analysed through linear regression models.

2.3.4. Reduction in abundance of different RRI groups

Within a set of secondary scenarios, we demonstrate the effect of reducing the abundance of species belonging to the three RRI groups on the BPc. Abundances were reduced from 10 to 90% for a specific RRI group for community BPc calculations. Furthermore, we created a random group by selecting species at random from the species list and considering the number of species found within the low RRI group as a reference. Random abundance reductions were performed as described for the extinction scenarios. The impact of abundance reductions of different vulnerability groups (RRI) on BPc can be explored by comparing the slopes and their relative position. All scenario responses were analysed through linear regression models.

3. Results

3.1. Validation of the RRI index

3.1.1. Effectivity of the RRI to represent vulnerability to trawling on a species level

To confirm the assumption that species with a low RRI should respond more strongly to trawling compared to higher RRI species, we correlated individual RRI scores of species with their observed regression coefficients. Considering all 54 species, we found a 0.22 r^2 correlation (Fig. 1A). When considering species with subsequently higher frequency of occurrence over the study area, the r^2 values increased up to 0.61 (Fig. 1B) for the 12 species that occurred at all sampling stations.

3.1.2. Modelled responses to trawling based on RRI grouping of species

The estimated mean response of species belonging to the three RRI groups using GLMM showed that species belonging to the Low RRI group, i.e., species with a low resistance and reproductive potential, mostly had a negative response to increases in trawling intensities (Fig. 2). This was followed by a slightly less negatively sloped relationship for the Moderate RRI species and a positive relationship for the High RRI species. The relationship for Low and Moderate RRI species was found to be statistically significant, while the estimated relationship for High RRI species was not (Table of model statistics see S6 and see supplementary Fig. S1 showing individual and mean responses of grouped species).

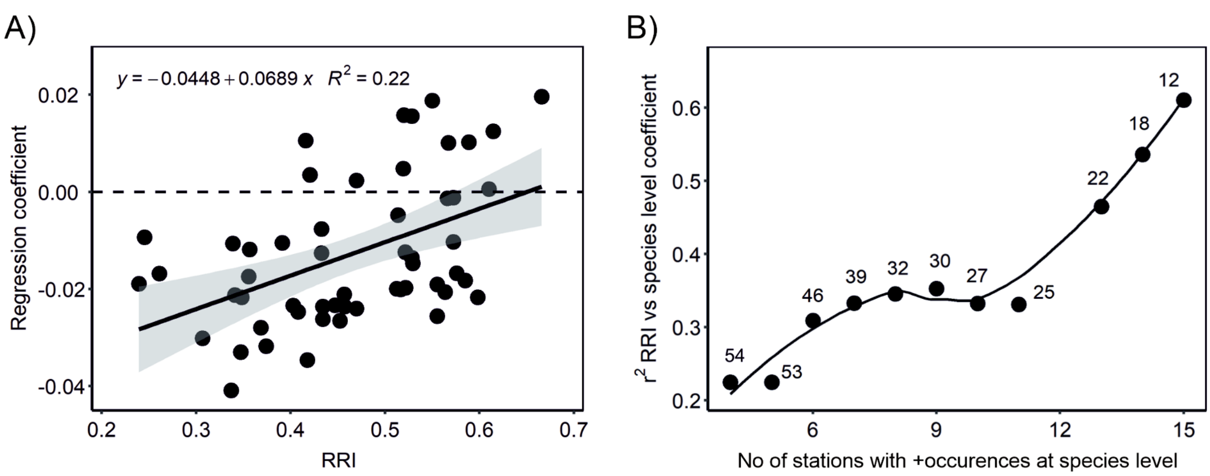

Fig. 1. A) Relationship between the RRI scores of benthic species and their regression coefficients from the observed relationships between trawling intensity and normalized biomass. B) Trend in the r^2 of the relationship featured in 2A consecutively excluding species that had many zero observations. The number above each data point indicates the number of species at that occurrence level, e.g., at the extreme right 12 species occurred at all 15 stations sampled and the relationship between RRI and coefficient had an r^2 of 0.61 (for regression statistics see S5).

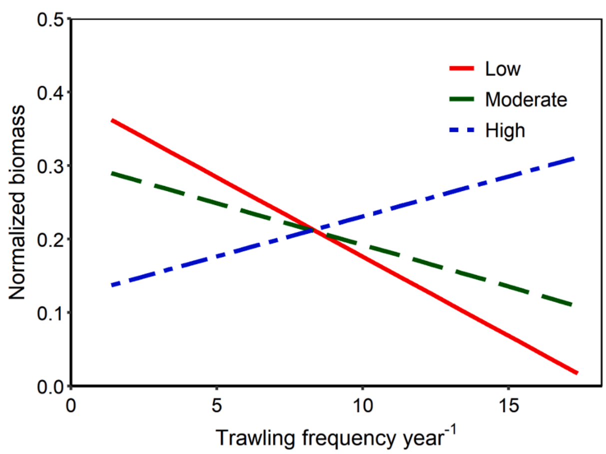

Fig. 2. Modelled mean responses of species belonging to the three RRI groups (Low; Moderate and High) using GLMM. The regression slopes were statistically significant for Low and Moderate RRI groups of species, while not for the High RRI group (see S6 for a detailed result table). Note that the High RRI group only contained three species.

3.1.3. Relationship of indices (RI, RPI, RRI) with trawling intensity on a community level

The individual species index scores, when calculated across the entire community, showed significant increases ($p < 0.05$) in all three indices in response to trawling (Fig. 3A-C). This indicates that the benthic communities in the case study area were increasingly composed of species with high resistance and recovery potential.

3.2. Linking vulnerability to function

3.2.1. Response of bioturbation potential (BPc) to trawling intensity

The BPc responded overall negatively to increased intensities of trawling in the case study area (Fig. 4a). When considering the different RRI groups, a strong negative relationship was found between the BPc and the low RRI species (i.e., highly vulnerable species), while BPc for moderate RRI species responded negatively, but with a less strong slope (Fig. 4b, S6). High RRI species, in contrast, increased their BPc over the trawling gradient.

3.3. Scenario modelling of the linkage between RRI and function

3.3.1. Directed extinction scenario of low and high RRI species

The simulation of removing species following the order of vulnerability, from lower to higher RRI scores in 10% steps from the station least

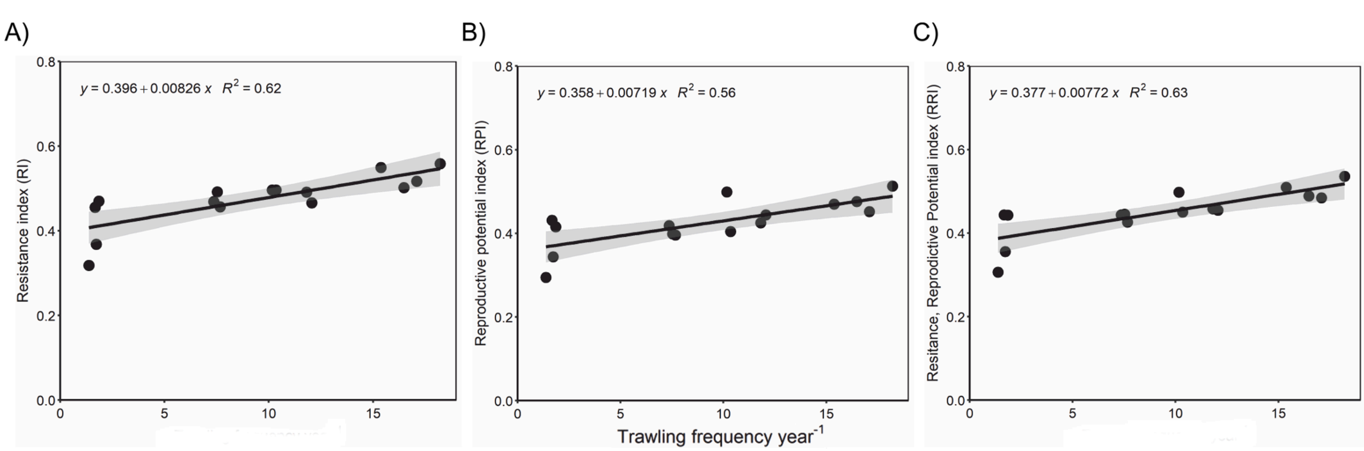

Fig. 3. Relationship between trawling intensity, as times swept per annum, and the three indicators A) physical Resistance Index (RI), B) the Recovery Potential Index (RPI) and C) the combined Resistance, Recovery potential Index (RRI).

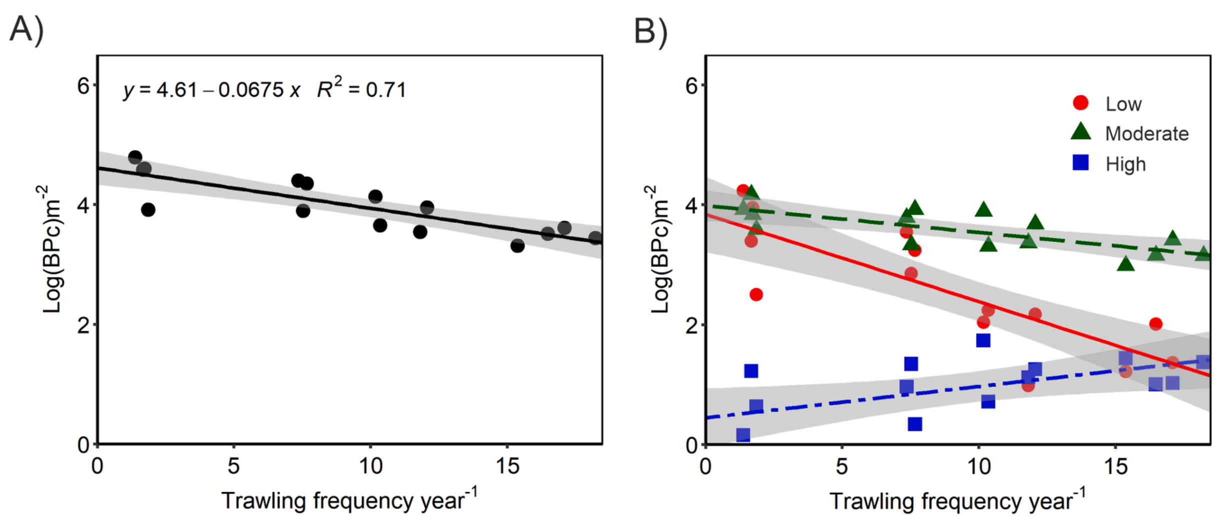

Fig. 4. A) Response of the log transformed bioturbation potential (BPc) with increasing trawling intensity as times trawled per annum. B) Responses of the log transformed bioturbation potential (BPc) for the three RRI groups. For more details about the regression results the reader is referred to S6.

affected by trawling, showed a strong negative effect on BPc (Fig. 5A). Reversing the removal of species from the community, from higher to lower RRI species, showed a less steep negative response. The simulated mean random removal of species demonstrated an intermediate negative response with the slope being located between the former two (Fig. 5A, S6).

3.3.2. Reduction in abundance of RRI groups and its effect on bioturbation

Within this scenario, the effect of reducing the abundance of different RRI groups by 10 to 90%, and its effect on BPc, was investigated. The abundance of respective groups was lowered, while keeping the contributions from the other groups constant, providing an estimate of how the different levels of reduction affected community BPc. There was a strong negative response in BPc when the abundance of species with low RRI scores was reduced i.e. vulnerable species (Fig. 5B). The reduction in abundance of the moderate RRI had a similar negative effect with a slightly less steep slope (Fig. 5B). The reduction in abundance of the high RRI group, as well as the reduction of random species, did not lower the BPc to the same extent as for the other two groups (Fig. 5B, see S6 for model statistics).

4. Discussion

4.1. Why introduce a new trait-based approach for fishing impact studies?

The impetus of creating a benthic resistance and recovery potential index (RRI) was based on the simple realization that a species represents a combination of traits that are interdependent of each other. It is the interplay of traits present by a species, with opposing, additive, neutral or synergistic effects, that determine its response to an external stressor. The introduced RRI index aims to pay tribute to the fact that trawling impacts ultimately occur at a species level and that a better understanding at this level would allow us to improve predictions on benthic communities' responses to trawling. Equally, as demonstrated within

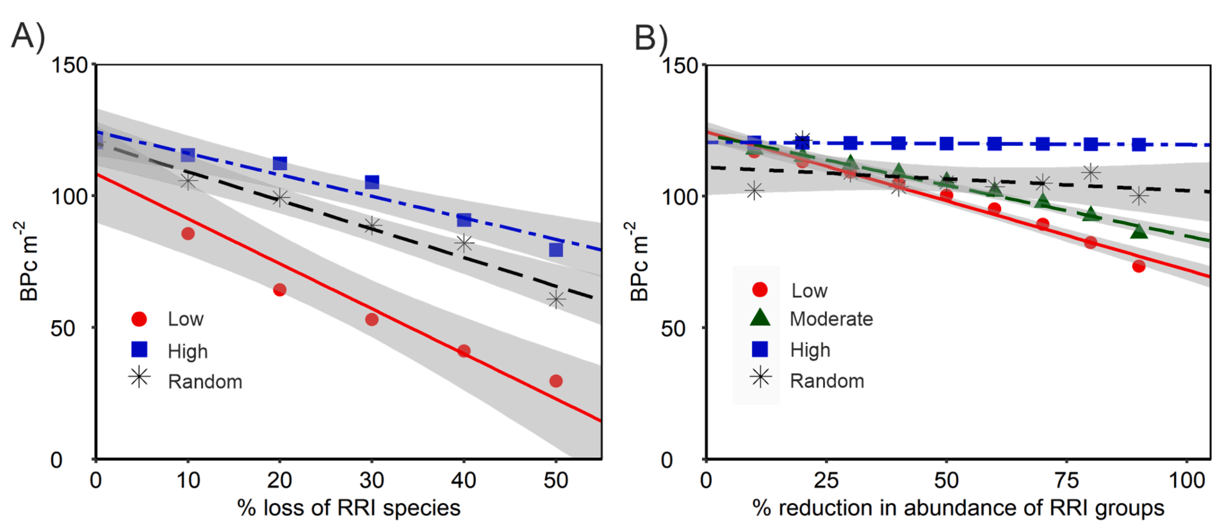

Fig. 5. Simulation scenarios taking the bioturbation potential (BPc) of the least impacted site as a baseline. A) Consecutive elimination of species from low to higher RRI species (Low, red solid line) and from high to lower RRI species (High, blue double dashed line), i.e., removal of 10–50% of the species. The grey dashed line (stars) represents the removal of species in a random order (mean of 999 permutations). Note that this graph is not referring to RRI groups. B) Scenario of reducing the abundance of different RRI groups on the bioturbation potential (BPc), from 10 to 90%, while keeping the contributions from the other groups constant. For the random response, we reduced the abundances of randomly selected species using the same number of species as in the low RRI group. The random reductions represent mean values of 999 permutations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this study, understanding the vulnerability on a species level can allow us to model or stress test the response of species, communities and functions to different pressure scenarios, e.g., by removing or reducing the most vulnerable species and assessing the consequences for ecosystem functions (e.g., such as bioturbation in the present study).

Another realisation that furthered the development of this index was that there are certain traits that are more directly linked to a stressor, while other traits respond only due to their association to those more directly linked traits. For example, a trait like life span could be regarded as indirectly related to the physical impact of the trawl gear, while living position, body texture or size are traits more directly linked. We therefore created additive indices, combining traits that reflected a directional trend towards the resistance and reproductive potential of a species. This type of additive index has previously been proposed in connection with trawling impacts by other authors e.g. Tyler-Walters et al. (2009) de Juan et al. (2009) and Bolam et al. (2014). All these use combinations of traits related to the physical resistance and reproductive potentials to calculate the overall sensitivity of organisms to trawling. The work by Bolam et al. (2014) is the most similar to the presented indices but differs through the traits included, the mechanistics of calculating the index scores and its application at a family level. More specifically, in Bolam et al (2014), trait modalities and sub-indices were not standardized, leading to an unbalanced contribution of these to the final vulnerability scores. The present study, implies a significant advance from the previous works in that it evaluates the validity of the proposed index by comparing it to empirical data and by providing a template for its multiple uses when applied at a species level. We believe that the development of this type of additive index has great potential and could be refined for other fishing impacts, habitat types, as well as for other human impacts or functions in general.

Similar to other trait-based indices, there is an element of subjectivity over which traits to integrate into the indices presented in this study. In this case, the traits were chosen based on the currently best available knowledge and mechanistic understanding about trawling impacts on muddy habitats and the ease of attaining such data for most species. It is though crucial to provide transparency over the index construction and to evaluate its performance in a validation process. In this study, we tried to address both of these aspects by comparing index performance to real observational data and by providing the required references of our trait data, including the amount of expert judgement that was used to populate the underlying traits matrix (see S1).

4.2. Validation of the resistance and recovery potential index

The mean response of species grouped after their vulnerability (RRI score) demonstrated the predicted pattern based on previous studies on trawling impacts on benthos (Jennings and Kaiser, 1998b). Thus, vulnerable species (Low RRI) respond strongly with a negative trend to trawling pressure, followed by moderately vulnerable species (Moderate RRI), while species with a high resistance and reproductive potential (High RRI) showed no significant response. Similarly, when comparing the individual slopes of observed species responses with their respective RRI index scores, we found a significant correlation between the two. The results of this part of the validation analysis provided confidence that the traits chosen for our indices and their scoring reflected the relative vulnerability or resilience of benthic species to trawling intensities. Nevertheless, the difference in fits of the correlations observed, depending on which species were included in the relationship, also revealed the predicaments over the biases of this type of validation. Species with rare occurrences over the trawling gradient often had many zero observations introducing uncertainty over estimated species responses (slopes) to trawling. Therefore, species with very few observations were removed from the analysis. However, these species may have been rare due to the trawling impact and thus we removed species strongly related to trawling impacts. For example, the sea pen *Virgularia mirabilis,* a highly vulnerable species with one of the lowest RRI scores recorded within our study, only occurred at the two least fished sites and thus could not be included in the validation analysis. On the contrary, other species included in the analysis showed trends based on few data points that were statistically not significant, potentially having introduced considerable bias into the evaluation analysis. Focusing the evaluation analysis only on the common species that occurred at most sites appeared to show the best fit between the observed regression slopes and our RRI index. Focusing the entire evaluation only on these species, however, would have reduced the generality of the analysis and would not have allowed the estimation of vulnerability (RRI) group responses as described at the beginning of the paragraph.

While the results of the validation analyses are encouraging, some details over the calculation of the RRI index need to be appreciated, in particular with respect to the scoring and weighting of the index and sub-indices. We choose to give each trait within each sub-index, the physical Resistance Index (RI) and the Recovery Potential Index (RPI), roughly the same influence on the final score. It is quite likely that some traits have a higher influence on the resistance or recovery potential of a species. However, currently, there exists limited understanding over the relative importance of individual traits and their contribution towards a function. For example, in the case of resistance, it is difficult to scale how much more important the trait living position is compared to the body morphology. Equally, we gave each of the two sub-indices the same weighting in calculating the final Resistance Recovery Potential Index (RRI) as we currently cannot determine which component makes a species more resilient to chronic trawling disturbance. As our understanding increases about trawling impacts, future versions of the indices could be weighted reflecting new emerging insights. One potential future route to explore this, especially with respect to the physical Resistance Index (RI), could be a more in-depth analysis of species-based responses from controlled trawling experiments assessing the instantaneous mortality caused by single or multiple fishing gears (Kaiser et al., 2006). The study of recovery and recruitment processes may, however, continue to pose a considerable challenge. Studies that have looked at recovery processes have done so mostly at the scale of small experimental plots, that tend to recover quickly, due to organisms moving in from the undisturbed adjacent areas. Recovery processes over larger spatial scales, i.e. fishing grounds, are expected to be distinct (Hinz et al. 2009). To date, little empirical data exists that could be used to effectively study the relative importance of different traits towards these larger scale recovery processes.

4.3. The application of the resistance and reproductive potential indices

The indices introduced within this study can be used in several distinct ways, a) they can be applied to investigate the changes in community resistance and reproductive potential as a response to a trawling gradient; b) they allow to explore the species contribution towards a response in terms of community biomass but also function, by the division of species into different resilient or vulnerability groups; and c) they can be used in stress test scenarios, by eliminating species or reducing their abundance/biomass depending on their vulnerability, and exploring its effect on linked ecosystem functions. The application of the indices to the fishing gradient study by Hinz et al. (2009) demonstrated well the multiple uses of the developed indices. All three indices (RI, RPI and RRI) showed significant positive responses to increasing trawling intensities on a community level. Thus, trawling, through the loss of more vulnerable species, increase the overall resilience of benthic communities in the Irish Sea with respect to their physical resistance and reproductive potential. While the term community resilience may have positive connotations depending on the context (Baggini et al., 2015; Knapp et al., 2001), in the present study it conveys the opposite. This is in line with many other studies on physical disturbances that found that communities in highly disturbed locations, anthropogenically or naturally, hold more resilient species adapted to this disturbance (de Juan et al., 2009; Sciberras et al., 2013). Resilience cannot be judged as a positive community aspect *per se* and the term should therefore be used with care with respect to the advocated preservation of resilience to affront ecosystem change (Gladstone-Gallagher et al., 2019). In general, our aim should be to strive to preserve functional resilience (Gladstone-Gallagher et al., 2019) through the protection of vulnerable species that make a considerable contribution through their abundance or biomass to a function. In this respect, our study found a strong impact of trawling on the bioturbation potential that experienced a loss of 81% along the trawling gradient studied. By having subdivided the species in vulnerability groups, we could explore the contribution of each group to this functional loss. Highly and moderately vulnerable species contributed with 55% and 45% respectively. Among those species with a high contribution towards bioturbation were, for example, the brittle star *Amphiura* spp., the irregular urchin *Echinocardium* spp. and the polychaete *Pectinaria auricoma*. In contrast, high resistant or low vulnerable species increased their biomass over the trawling gradient and compensated to a small extent the loss of the two other groups. Without this compensation, total bioturbation potential loss along the trawling gradient would have been 3% higher. The results of this study demonstrate that a large part of the bioturbation function was linked to vulnerable species and that their removal had a considerable effect on the provision of this function. Due to the benthic community Bioturbation Potential index (BPc) being a proxy for bioturbation, care should be taken when considering these results, as it is currently unknown how well the index reflects real bioturbation processes. Nevertheless, in the absence of empirically measured bioturbation rates for different species, it is currently the best available estimate.

The scenario analysis performed on the least impacted site of the Irish Sea case study demonstrated the strength of the index for a data poor scenario, where only a few benthic samples are available. The simulation of sequential species loss from both the most vulnerable to the most resilient, and vice versa, reflected well the trends identified in the observed data, demonstrating that similar conclusions about the importance of vulnerable species and their link to bioturbation could have been drawn from sampling one single site.

5. Conclusion

We feel that despite the adolescent nature of our index, it is sufficiently advanced to be discussed, applied and hopefully developed further by the scientific community. The principal idea to move away from descriptive community wide trait-based analysis towards a more focused and mechanistic trait-based approach, which appreciates the integrate nature of traits unified in a species, should enable scientists to develop new approaches that will be more universal and potentially have higher predictive power. With respect to the presented RRI index and its sub-indices, it means that the vulnerability and the functional potential (e.g., bioturbation) of benthic communities can be estimated for almost any location provided one has the associated traits data for the local species' pool. Using traits of individual species in this way, allows for stress testing communities through developing scenarios that may reflect future environmental change or management decisions (e.g., changes in fishing effort regulations). Within our study, we presented an index that was directed toward the physical impact of trawling, but similar indices could be developed for other fishing gears or stressors, such as climate change or eutrophication. As the introduced indices are conceptually simple, they should be easily adaptable to other scenarios and situations. To conclude, we demonstrated that, through our indices, new insights into the link between species vulnerability and function with regards to trawling impacts can be gained. While further testing and development of our index will be required, we hope that our approach will lead to a new scientific discourse about the use and application of ecological traits and their potential to increase our understanding of functional ecology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107692.

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