

RESEARCH ARTICLE

Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats

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Funding information

David and Lucile Packard Foundation; Walton Family Foundation; Food and Agriculture Organisation of the United Nations; The Alaska Seafood Cooperative; American Seafoods Group; Blumar Seafoods; Clearwater Seafoods; Espersen Group; Glacier Fish Company LLC; Gorton's Inc.; Independent Fisheries Limited; Nippon Suisan (USA), Inc.; Pacific Andes International Holdings, Ltd.; Pesca Chile S.A.; San Arawa, S.A.; Sanford Ltd. N.Z.; Sealord Group Ltd. N.Z.; South African Trawling Association; Trident Seafoods; FP7, Grant/Award Number: 312088

Handling Editor: Rute Pinto

Abstract

1. Bottom trawl fisheries are the most widespread source of anthropogenic physical disturbance to seabed habitats. Development of fisheries-, conservation- and ecosystem-based management strategies requires the selection of indicators of the impact of bottom trawling on the state of benthic biota. Many indicators have been proposed, but no rigorous test of a range of candidate indicators against nine commonly agreed criteria (concreteness, theoretical basis, public awareness, cost, measurement, historical data, sensitivity, responsiveness, specificity) has been performed.
2. Here, we collated data from 41 studies that compared the benthic biota in trawled areas with those in control locations (that were either not trawled or trawled infrequently), examining seven potential indicators (numbers and biomass for individual taxa and whole communities, evenness, Shannon–Wiener diversity and species richness) to assess their performance against the set of nine criteria.
3. The effects of trawling were stronger on whole-community numbers and biomass than for individual taxa. Species richness was also negatively affected by trawling but other measures of diversity were not. Community numbers and biomass met all criteria, taxa numbers and biomass and species richness satisfied most criteria, but evenness and Shannon–Wiener diversity did not respond to trawling and only met few criteria, and hence are not suitable state indicators of the effect of bottom trawling.
4. *Synthesis and applications.* An evaluation of each candidate indicator against a commonly agreed suite of desirable properties coupled with the outputs of our meta-analysis showed that whole-community numbers of individuals and biomass are the most suitable indicators of bottom trawling impacts as they performed

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well on all criteria. Strengths of these indicators are that they respond strongly to trawling, relate directly to ecosystem functioning and are straightforward to measure. Evenness and Shannon–Wiener diversity are not responsive to trawling and unsuitable for the monitoring and assessment of bottom trawl impacts.

KEYWORDS

beam trawl, ecosystem approach to fisheries management, hydraulic dredge, meta-analysis, otter trawl, scallop dredge, systematic review

1 | INTRODUCTION

Bottom trawls, here defined as any towed bottom fishing gear including otter trawls (OT), beam trawls, scallop dredges and hydraulic dredges (HD), are used to catch fish and shellfish living in, on or near the seabed (Sainsbury, 1986). Bottom trawling is by far the largest source of human physical disturbance in the marine environment, but also makes an important contribution to global food supply, accounting for 19–25 M tonnes of annual fish landings (Amoroso et al., 2018). It is therefore important to quantify trawl impacts to assess sustainability and guide management in the context of wider ecosystem management and conservation (Clark et al., 2016; McConnaughey, Hiddink, Jennings, Pitcher, et al., 2020).

Reductions in faunal biomass, numbers and species richness (Sciberras et al., 2018) and selection for communities dominated by short-lived fauna have been documented in response to bottom trawling (van Denderen et al., 2015). This can lead to changes in community production, trophic structure and ecological function (Duplisea, Jennings, Malcolm, Parker, & Sivy, 2001; Hiddink et al., 2006) and can cause reductions in the prey abundance of commercial fish species (Collie et al., 2017).

When protection of habitats and their associated biota are the management objectives, the implementation of ecosystem-based fisheries management requires information on the distribution and impact of bottom trawling, and status of biota and habitats (Rijnsdorp et al., 2016). This information enables assessment of the intensity of potential impacts which can be used to help society achieve an accepted balance between fisheries production and environmental protection (Rice, 2005, 2011). Evaluating the consequences of management interventions requires indicators of the state of seabed environment. Furthermore, commitment to marine policies such as the European Marine Strategy Framework Directive and evaluation of descriptors therein such as 'seafloor integrity', requires the development of indicators of trawling impacts that capture changes in the structure and function of benthic ecosystems (Rice et al., 2012).

Here we define 'state' as the condition of the ecosystem, while impact is the change in this state in response to trawling pressure relative to its untrawled reference level. State indicators to support the management of bottom trawling impacts on benthic ecosystems should satisfy a range of requirements (Jennings, 2005; Rice & Rochet, 2005). The theoretical basis for the cause-and-effect between trawling and the indicator should be easily understood and intuitive, as this would

facilitate acceptance and support among stakeholders and the wider public. Effective indicators should quantify ecologically important parameters that relate to changes in the structure and functioning of the benthic ecosystem, both of which correlate closely to benthic biomass (Hiddink et al., 2006; Queiros et al., 2013). The parameter should be easily measured, sensitive to fishing impacts and provide rapid and reliable feedback on the efficacy of management actions. Changes in the indicator should be specific to the effect of trawling rather than confounded by environmental variation, unless other sources of variation are understood, quantifiable and can be accounted for. Attribution of causality for changes in ecosystem properties is challenging, given that all the changes in trawled communities are not necessarily responses to trawling. Finally, indicators for which (historical) data are available and that are cost-effective to generate are preferable. In practice, the best indicators will exhibit a strong response with a low variance, indicating a high specificity of the response, and will include only small effects of other environmental variation (Maxwell & Jennings, 2005).

A number of indicators of the impact of trawling on benthic ecosystems have been proposed, including numbers, biomass, species richness, measures of diversity and trait-based community descriptors of benthic biota (e.g. Rijnsdorp et al., 2016; van Loon et al., 2018). However, the utility of many commonly used indicators, such as species richness, has not been tested and no systematic comparison of the sensitivity nor specificity of different indicators has been performed. Such tests are needed given that some of the currently used indicators are in fact insensitive to trawling, and respond instead to environmental gradients (e.g. Gislason, Bastardie, Dinesen, Egekvist, & Eigaard, 2017).

Performance of indicators can be assessed by comparing their responses to a known pressure. Searches of the literature revealed many trawling impact studies where the benthic community is compared in two or more areas with contrasting, although not always quantified, trawling intensity (e.g. Engel & Kvitek, 1998; Sciberras et al., 2013). These control-impact studies provide an opportunity to compare the sensitivity, responsiveness and specificity of different indicators. Here, we perform a systematic evaluation of potential state indicators of bottom trawl impacts by testing each indicator against the criteria defined by ICES (2005) and Rice and Rochet (2005): concreteness, theoretical basis, public awareness, cost, measurement, historical data, sensitivity, responsiveness and specificity (Table 1). To test sensitivity, responsiveness and specificity, we perform a meta-analysis of comparative control-impact studies

TABLE 1 Criteria for the selection of state indicators from ICES (2005) and Rice and Rochet (2005)

Criteria	Description of indicators
Concreteness	Directly observable and measurable property of physical/biological world rather than reflecting abstract properties which can only be estimated indirectly
Theoretical basis	Link between pressure and indicator based on well-defined and validated theoretical links
Public awareness	Public understanding consistent with its technical meaning. Nature of what constitutes 'serious harm' is widely shared
Cost	Uses measurement tools that are widely available and inexpensive to use
Measurement	Measurable in practice and in theory, using existing instruments, monitoring programmes and analytical tools, and on the time-scales needed to support management. Minimum or known bias, and signal should be distinguishable from noise
Historical data	Supported by a body or time series of data to aid interpretation of trends and to allow a realistic setting of objectives
Sensitivity	Trends should be sensitive to changes in the ecosystem state, pressure or response that the indicator is intended to measure
Responsiveness	Responsive to effective management and provides rapid and reliable feedback on the consequences of management
Specificity	Responds to the properties they are intended to measure, rather than to other factors and/or it should be possible to disentangle the effects of other factors from the observed response

to compare the effect of different trawl gears, in different habitats and on different indicators (numbers and biomass for both individual taxa and whole communities, and three measures of diversity), while the other criteria are assessed using judgement by the authors.

2 | MATERIALS AND METHODS

Data were collated from published comparative studies of the effects of bottom trawling on seabed habitat and biota following a systematic review protocol, thereby including all available studies and avoiding selection bias (Hughes et al., 2014). The methods were designed to identify and collate evidence from comparative control-impact studies to identify changes in state of benthic biota resulting from mobile bottom fishing. The search strategy is documented in Hughes et al. (2014), which specifies the databases searched and search terms used in detail. Our literature search period finished in 2014 and no studies beyond that date are included here. Studies were only included in the meta-analysis when they compared benthic invertebrates in two comparable areas, where one area was commercially trawled and the other was not trawled or was only lightly trawled. This excludes studies where areas were experimentally trawled, and comparative gradient studies where many different levels of quantified trawling effort were sampled. Included studies were restricted to those performed on the continental shelf and upper slope (0–400 m) and to those reporting numbers, biomass or diversity of benthic communities, species, genera or families of in-fauna or epifauna. Studies needed to report the mean and a measure of variation, such as a standard deviation or confidence interval, to be included in the meta-analysis. Our analysis of comparative studies assumed that other environmental covariates did not correlate or vary with trawling intensity at the scale of the experiments. Studies where this assumption was apparently violated in our assessment of study quality, such as in Hixon and Tissot (2007) where the depths of trawled and control areas diverged by up to 180 m and the species composition in the two areas diverged greatly, were not included in

the analysis as this would confound environmental with trawling effects (see Text S1). The meta-data extracted for each study (including location, depth, trawl gear type, habitat) are provided in Table S1. Gear types in the studies were classified as OT, beam trawls (BT), towed dredges (TD) and HD. Further details of the methodology are available in Hughes et al. (2014).

A subset of 10 publications reported on 14 studies in which trawling was not continuous but instead was (a) stopped in the trawled area or (b) stopped in the control area and continued in the trawled area. If trawling was stopped in the fished areas, we only used data from the first point in time, as soon as possible after trawling was stopped, as this represents the maximum measured effect of fishing. If trawling initially occurred in the control area and was then stopped, we used the last point in time during the study period. Although this approach may underestimate the effect of trawling, excluding these studies would have removed almost all studies on biogenic habitats. We address the extent of this underestimate in our interpretation of results. Trawling intensity was not quantified in most studies, but where trawling frequency was quantified, the mean swept-area-ratio was 3.36 year⁻¹ in the trawled area (range: 0.2–12.9) and 0.1 year⁻¹ in the control area (range: 0.0–0.4).

2.1 | Analysis

Studies were analysed using weighted meta-analysis via linear mixed-effects models (a standard approach for meta-analysis, using `rma.uni` function in R package `METAFOR`, Viechtbauer, 2010) with the log response-ratio ($\ln RR$) for the candidate indicator (I) as the response variable, calculated as $\ln(I_{\text{trawled}}/I_{\text{control}})$, where the log-transformation helps to homogenize and normalize the residuals. Studies were weighted by the inverse of variance of the original study, where the combined variance per study was calculated as in Borenstein, Hedges, Higgins, and Rothstein (2009). A significant effect of trawling is present when the 95% confidence intervals of $\ln RR$ do not overlap with $\ln RR = 0$.

2.2 | Response measures (*I*) for calculating InRR

Studies reported many different metrics for benthic fauna, including numbers and biomass for individual taxa (at different levels ranging from species to phylum) and for whole communities. Candidate indicators examined were: numbers and biomass by taxa and for the whole community, species richness, Shannon–Wiener diversity H' , Margalef's d and Simpson's dominance D and evenness J' . Other potential indicators were reported in a few studies but not included in this analysis because fewer than five studies reporting their effects were available and they fell outside the scope of the systematic review (e.g. ABC plots in Vergnon & Blanchard, 2006 and TDI in de Juan & Demestre, 2012). All indicators were used as reported in the studies. Responses for 'taxa' indicate the responses of the abundance of all individual taxa that were reported in the studies (rather than the response of the summed abundance of taxa, which is already reported as numbers or biomass for the whole community). Taxon-level analyses estimated the mean of the responses of individual taxa, while community-level analyses estimate the response of whole-community numbers or biomass. To maximize the statistical power of our analyses, we combined the response of species richness and Margalef's species richness index in a single analysis (here called species richness) because these outcomes measure very similar responses such that the magnitude and direction of a trawling effect can be assumed to be similar. InRR examines relative changes and therefore difference in the magnitude of species richness and Margalef's d is unimportant for the results. Simpson's dominance D was converted to evenness J' by assuming that $J' = 1 - D$ (Gray & Elliott, 2009) and analysed in a single analysis with J' .

2.3 | Environmental covariates determining the effect of trawling in comparative studies

Environmental factors play a role in determining the magnitude of effect of trawling on seabed biota. Thus we evaluated the influence of a number of environmental variables, at the between-study level, by including them individually as covariates in the mixed-effects meta-analysis. The significance of each of the covariates in isolation was assessed using the p -value of the Q_M test statistic (Borenstein et al., 2009). The effect of trawling on benthos is likely to increase when the fraction of animals depleted (d) by a trawl pass is high, and is likely to decrease when recovery from trawling (r) is fast. Pitcher et al. (2017) showed that the effect of trawling on benthic biomass is proportional to the d/r ratio when population growth is determined by logistic population dynamics. Therefore, we examined a number of environmental covariates that are related to d and r , and may thus influence both the magnitude of depletion and the rate of recovery following trawling.

Values of r are expected to depend on variables that affect growth rates of individuals and populations. Thus, the following covariates for r were examined: primary production (PP) estimated from the vertically generalized productivity model ($\text{mg C m}^{-2} \text{ day}^{-1}$; Behrenfeld & Falkowski, 1997) and particulate organic carbon flux to depth (POC flux, $\text{g C}_{\text{org}} \text{ m}^{-2} \text{ year}^{-1}$; Lutz, Caldeira, Dunbar, & Behrenfeld,

TABLE 2 The number of studies for macrofauna by gear and habitat. Otter trawls (OT), towed dredges (TD), hydraulic dredges (HD). The depletion per trawl pass, d , is the fraction of biota that is killed or removed in the trawl path by the pass of a trawl

	OT	TD	HD
Biogenic	1	3	—
Gravel	1	12	—
Sand	6	5	1
Sandy mud/muddy sand	2	—	2
Mud	8	—	—
Depletion per trawl pass d , composite value for whole communities for all habitats (Hiddink et al., 2017)	0.06	0.20	0.41

2007) as proxies for energy availability; mean sea bottom temperature (SBT) calculated from monthly mean bottom temperature for 2009–2011 (<http://marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-009-011-017.pdf>); depth in metres (from GEBCO, <https://www.gebco.net/>, if not reported in the original study); and habitat type. Because of a strong negative correlation between SBT and PP in the selected studies ($r = -0.61$, $t = -2.9$, $p = 0.0115$), SBT was not used in the final analyses. Habitat types were classified as biogenic habitats, gravel, sand, muddy sand/sandy mud and mud. A second test of substrate type was done using continuous percentages of gravel, sand and mud fractions of the sediment, which were derived from the source studies by converting the sediment description to the Folk classification (Folk, 1954) where needed, and then converting the Folk classification to percentages based on the means in each Folk category.

In addition to analyses using covariates of r , we also conducted analyses using covariates of the d/r ratio, using gear-specific d estimates from Hiddink et al. (2017; Table 2). The effect of trawling is expected to increase with water depth due to the lower levels of natural disturbance in deeper water and the corresponding increase in the relative abundance of individuals with slower life histories (low r), so $d \times \text{depth}$ was examined as a covariate for d/r , with depth expressed as a negative number. Some of these covariates are ad hoc approximations of relationships that are likely to be more complex. Habitat categories and gear type (OT, BT, TD and HD) were also examined as categorical variables, but a category was only included in the analysis when the number of studies was >2 . The effects of environmental covariates on H' and J' were not examined because of the limited number of replicate studies that reported these response variables.

3 | RESULTS

In total we found 41 control–impact studies with 18 studies reporting the effect of otter trawling, 20 studies of TD and three studies of hydraulic dredging (Table 2). No studies reporting the effect of beam trawls were identified. All included studies were carried out in non-tropical waters, with a large concentration of studies in W

Europe and NE USA (Figure 1). All studies were carried out on the continental shelf, with only three studies at depths > 100 m.

Significant effects of trawling were detected on the indicators 'numbers of individuals in individual taxa' (mean: -35%, for confidence intervals see Figure 2), 'numbers of individuals in whole communities' (-43%) and for whole-community biomass (-59%, with the lowest upper confidence limit), but not for the biomass of individual taxa (-14%, Figure 2, although using a less conservative 90% confidence interval also results in a significant effect for taxa biomass). The effect on species richness was smaller but significant (-21%), while the effects on the other measures of community diversity (J' and H') were small and not significant, with evenness J' increasing with trawling (Figure 2).

Several environmental covariates explained a significant amount of variation in the response of indicators, although most did not. There was a significant negative relationship between the ratio of the depletion to primary production ratio ($\log_{10} d/PP$) and the lnRR of the number of individuals in the community ($p = 0.014$, Figure 3c) and species richness ($p = 0.043$, Figure 3e), with the effect of trawling being stronger for fishing gears that cause a higher depletion and the effect being weaker in areas of high primary production (Table S2). This means that the impact of trawling is larger for gears that deplete a larger fraction of fauna, such as dredges, and in areas with a lower food supply to the benthos where recovery is likely to be slower. Although the effects of gear and habitat on lnRR were not significant for most outcomes (Table S2), Figure 4 shows a broadly consistent

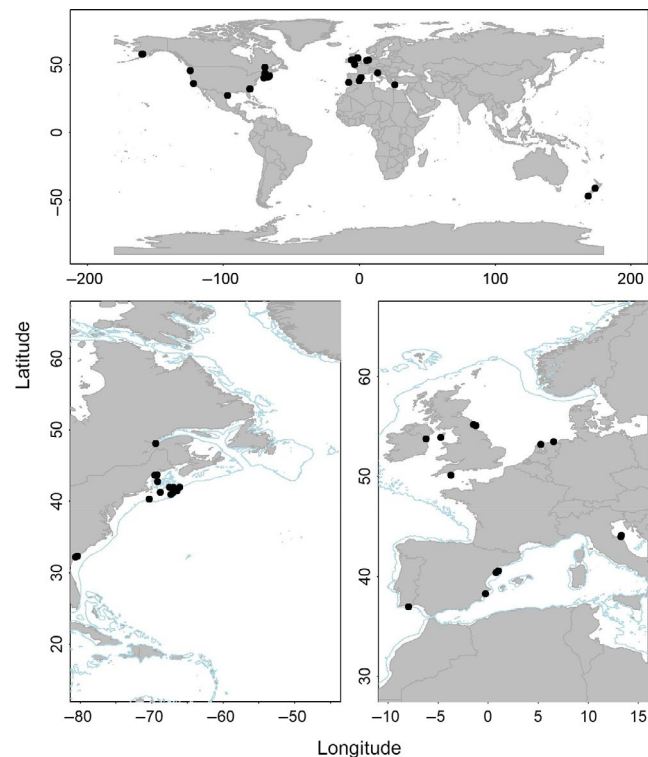


FIGURE 1 Maps of the locations of the studies. The finer-scale maps of the northwest and northeast Atlantic give more detail for two areas having a concentration of studies. The 200 m depth contour is shown in blue

pattern across the different indicators with stronger effects on coarser and biogenic sediments and for dredges that penetrate the sediment more deeply. For the numbers of individuals of individual

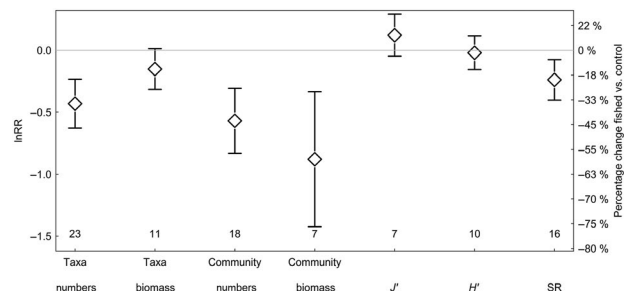


FIGURE 2 Mean response to trawling log response-ratio (lnRR) and 95% confidence intervals for the indicators. If the confidence interval overlaps 0 the effect was not significant. N (=number of studies reporting on each indicator) is given under each bar. The right-hand axis gives % changes for ease of interpretation. J' : evenness, H' : Shannon-Wiener diversity index, SR: species richness. Responses for taxa indicate the mean of the responses of the individual taxa that were reported in the studies

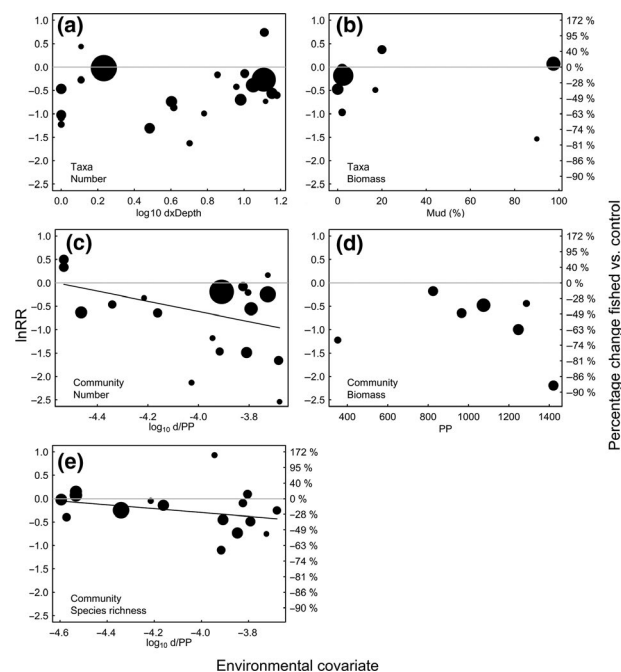


FIGURE 3 The effect of the best-fitting continuous explanatory covariates on the effect of trawling. The panels show the lnRR of (a) taxa numbers as a function of the product of depletion and depth, (b) taxa biomass as a function of mud content, (c) community numbers as a function of the ratio of depletion over primary production, (d) community biomass as a function of primary production, and (e) species richness as a function of the ratio of depletion over primary production. The effect of the best-fitting continuous explanatory covariates on the effect of trawling. Bubble sizes are proportional to inverse-variance weighting of the study, where larger bubble size indicates smaller uncertainty. Significant relationships are indicated with a black line. d = Depletion (fraction of animals depleted by a trawl pass, which depend on the gear type, d values given in Table 2), PP = primary production ($\text{mg C m}^{-2} \text{ day}^{-1}$)

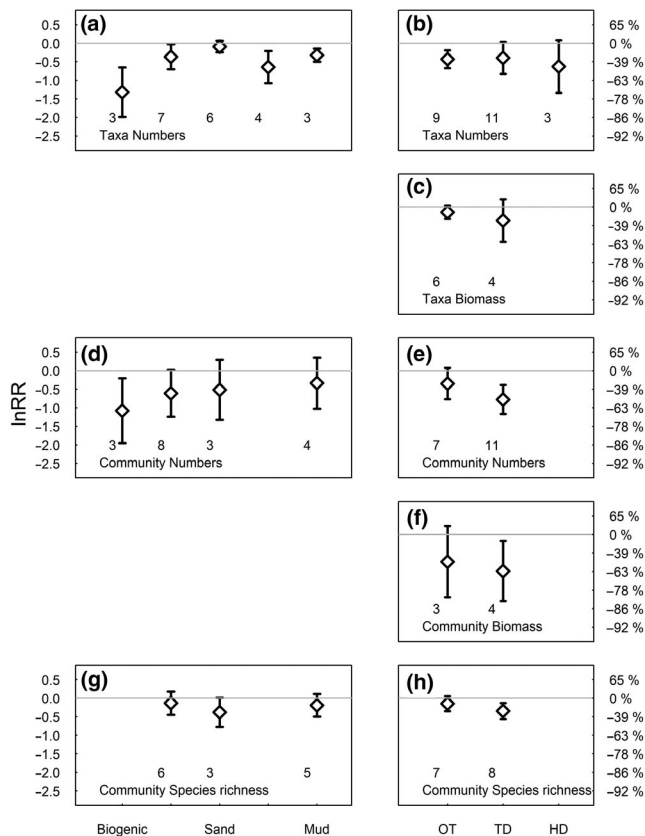


FIGURE 4 Meta-analysis results by gear (b, c, e, f, h) and habitat (a, d, g). Figures are only given if $N \geq 3$ for at least two categories. HD, hydraulic dredge; mS&S, muddy sand and sandy mud; OT, otter trawl; TD, towed dredge. Missing panels had too few studies. The significance of the differences is presented in Table S2, and can be inferred from whether confidence intervals overlap

taxa, the effect of habitat was significant, with strong effects on biogenic habitats (which are mostly dredged, Table 2), smaller effects on muddy sediments (which are mostly otter trawled, Table 2) and the weakest effects on sand (Figure 4a). We could not disentangle the gear-habitat interaction in our analysis because of a lack of studies.

4 | DISCUSSION

Community numbers and biomass met all performance criteria (9/9), taxa numbers (8/9) and biomass (4/9) and species richness (8/9) met many criteria. Whole-community numbers and biomass satisfied most criteria and are, therefore, the most suitable for monitoring the effect of bottom trawling on seabed biota. Evenness (2/9) and Shannon–Wiener (1/9) diversity did not respond to trawling and met few criteria, and hence are not suitable state indicators for monitoring and assessing the effect of bottom trawling on the seabed biota (Table 3).

Strengths of whole community numbers and biomass as indicators are that they respond strongly to trawling, reflect aspects of ecosystem functioning and are straightforward to measure. All of these indicators are expensive to measure as they require sampling of the seabed

from vessels, but benthic sample processing is substantially cheaper for whole-community biomass and numbers than for the other indicators because no identification of fauna is required. Taxa numbers and biomass and species richness also met most criteria. The whole-community biomass-based indicator also has the particular advantage that it is likely to correlate more closely to ecosystem functioning than numbers and richness, because it incorporates the effects on body size and age structure, as well as numbers and energy flow through food webs and other ecosystem processes that are linked closely to biomass (Hiddink et al., 2006; Queiros et al., 2013). However, these separate properties are confounded in the whole-community biomass variable because communities with a variety of different size and age compositions can end up with the same value for the indicator, yet might require different management interventions or fishery practices to provide desired outcomes for fishery operations or ecosystem functions (McConnaughey, Hiddink, Jennings, Suuronen, et al., 2020).

Good indicators of effect of bottom trawling on the seabed biota will respond specifically to the impacts of bottom trawling and, when necessary, it should be possible to disentangle these responses from the responses to other environmental pressures, e.g. using Before–After Control–Impact designs (e.g. Gislason et al., 2017; Pitcher, Burridge, Wassenberg, Hill, & Poiner, 2009). Our results show that the response of taxa- and community-numbers and species richness varied with other environmental factors, demonstrating that the effect of trawling can be disentangled from the effects of other factors and revealing a high level of specificity for these indicators. However, in some of the underlying studies, the control area was not only closed to bottom trawl fishing but also had different exposure to other human activities. For example, Blyth, Kaiser, Edwards-Jones, and Hart (2004); and Simpson and Watling (2006) both compared trawled areas with areas that were untrawled but had high levels of pot-fishing activities. This weakens our conclusions about the specificity of the indicators, as the effect of trawling is confounded with the effect of other activities. We found that bottom trawling had the greatest effects on community numbers and species richness for trawl gear types when a pass of the gear removes a larger fraction of fauna, and smaller effects in areas that have higher primary production. This means that similar amounts of fishing will affect less productive communities more relative to more productive communities, as previously observed for trawl impact studies (Hiddink et al., 2017). The effects of trawling were particularly strong in biogenic habitats, in coarse sediment habitats trawled by dredges, and weaker in finer sediment habitats trawled by OT. Similar effects were found in a meta-analysis of comparative gradient studies (Hiddink et al., 2017).

The responses of the indicators to trawling may be correlated. Bottom trawling reduces the number of individuals for many species as well as shifting the body-size distribution to smaller sizes, together leading to a reduction in population biomass (e.g. Hiddink et al., 2006). These responses of many individual taxa generate the whole-community number and biomass response. The reduction in species richness in response to trawling is linked to reductions in taxa numbers that result in a lower probability of species detection in relatively small sampling areas (rather than actual disappearance of species on larger scales) and the response of the species richness

indicator therefore correlates to changes in community and taxa abundance (Gislason et al., 2017). The responses of evenness J' and Shannon–Wiener diversity H' are driven by relative changes in abundance between different taxa, which depend on competitive and predatory interactions of the species in the community and differ between regions and environments (Svensson, Lindegarth, Jonsson, & Pavia, 2012), and this explains why the observed responses in our meta-analysis are not significant. Differences in the depletion per trawl pass between taxa (Sciberras et al., 2018) can also play a role, and are not easy to predict (Sciberras et al., 2018).

The extent to which the responses of indicators show similar directions and magnitudes depends on how strongly the responses of the individual taxa covary, and on the dominance pattern of population biomasses by taxa. Observed patterns indicate that sensitive species make up a large fraction of the biomass in untrawled ecosystems. For example, because of their large size, the biomass of the soft coral dead man's fingers *Alcyonium digitatum* or large clams (e.g. *Arctica islandica*) can be very high and make up >50% of all biomass in some untrawled areas (Rijnsdorp et al., 2018). When trawled or disturbed, such large species are often strongly reduced in biomass, thereby increasing evenness of the community (Kimbri & Grosholz, 2006) and substantially reducing total community biomass, while the magnitude of the reduction in numbers is modest. Other, generally smaller, taxa may benefit to some extent and increase due to a reduction in competition and/or predation, without fully compensating for the decrease in biomass of the (larger) sensitive species. The observation that community numbers and biomass responded more strongly than mean taxa numbers and biomass suggests that such compensatory responses are weak. In the taxa level analysis, the effect of trawling on each taxon is equally weighted regardless of its contribution to community biomass, and this results in a smaller overall effect because the decrease in high-biomass sensitive species has a much smaller effect on the value of the indicator.

Biomass-based indicators capture effects on body size and age structure as well as numbers. These properties of the community affect the energy flow through food webs and other ecosystem processes, meaning that they are likely to correlate to the functioning of the ecosystem. Biomass-based indicators are also less likely to show sudden jumps in response to recruitment pulses that are unrelated to trawling, because even though recruits may be numerically abundant, they usually contribute very little to total biomass. An unimpacted, and naturally functioning, benthic community in a stable environment has a size-, age- and longevity-distribution that is normally characterized by a large biomass of old and large biota (Hiddink et al., 2019; Rijnsdorp et al., 2018). Of the indicators considered, whole-community biomass is most likely to reflect the difference between this type of unimpacted community and one that is trawled.

The studies upon which our conclusions are based were obtained using a systematic review approach and therefore represent all globally available studies that satisfied the selection criteria, but they do not necessarily provide a balanced sample of all habitat \times gear combinations. The conclusions drawn here are most

applicable to the habitats represented in the underlying sources, although because of the general nature of the indicators examined, and the generality of the responses of seabed biota to trawling (Hiddink et al., 2017), there is no reason to assume that the general ranking of indicator performance would vary substantially among geographies and habitats. For these reasons we recommend community biomass as a globally applicable state indicator for monitoring and assessing the status of seabed biota impacted by trawling. Applications would include measuring and reporting comparative seabed status in trawled and untrawled areas or across gradients of trawling intensity, and describing temporal changes in seabed status (e.g. rates of depletion or recovery following initiation or cessation of trawling).

A substantial amount of the observed variation in benthic states was explained in our analysis, and much of the remaining variation is likely to be due to variation in the actual trawling intensity at both control and impact locations, as well as variations in gear size, weight, selectivity and rigging. Other reasons for the large variation (indicated by 95% CI) around the observed means are the substantial spatial variation in abundance of benthic invertebrates at the scale of the sampling gear, and differences in environmental conditions between trawled and control areas that were not reported or may not have been appropriately controlled for in some studies. As a result, the statistical power to detect effects was low, and the environmental covariates that we tested only explained a significant amount of variation in three out of 70 covariate–indicator combinations. Some low-intensity trawling occurred at control locations in some studies, although at much lower intensities than at impact locations, and will potentially lead us to underestimate of the effect of trawling. Other factors contributing to a potential underestimate of the trawling effect include the history of fishing disturbance as depletion of community abundance will be higher in unfished areas relative to previously fished areas (Sciberras et al., 2018) and the inclusion of some studies where either the control or the impacted site were on a recovery trajectory. Such underestimates should however not have affected our assessment of the relative utility of the different indicators.

4.1 | Synthesis and applications

We show that community numbers of individuals and biomass are the most suitable indicators of trawling impacts as they performed well when evaluated across the full suite of criteria. Strengths are that they respond strongly to trawling, correlate closely to ecosystem functioning and are straightforward to measure. When state indicators that respond to the effects of trawling are needed to represent the structure and function of benthic habitats, such as is required by the Marine Strategy Framework Directive (Rice et al., 2012) and the Marine Stewardship Council sustainability standard (Marine Stewardship Council, 2018), it is preferable to use community biomass rather than numbers, because the biomass response incorporates the effects of trawling on body size and age structure, as

TABLE 3 Scoring of the candidate state indicators against each of the criteria described in Table 1. ✓ = 'meets criterion'. × = 'does not meets criterion'. Scoring of measurement, historical data, sensitivity, responsiveness and specificity are entirely or partly based on analyses presented in this paper. Other criteria as scored by consensus of the authors based on existing knowledge from the literature

Indicator	Numbers of individual taxa	Biomass of individual taxa	Community number of individuals
Concreteness	✓. Predominantly for taxa that are large and conspicuous, as their numbers are directly observable (but not for colonial animals like corals)	✓. Predominantly for taxa that are conspicuous, as biomass is directly observable	✓. Most strongly when community comprises larger individuals that are directly observable (but not for colonial animals like corals)
Theoretical basis	✓. Relevant to quantity of biota and links to pressure supported by models of trawl impacts (Hobday et al., 2011). Numbers of individuals by taxa to some extent linked to ecosystem function	✓. Relevant quantity of biota and links to pressure supported by models of trawl impacts (Pitcher et al., 2017). Biomass by taxa positively linked to functional role	✓. Relevant to quantity of biota and links to pressure supported by models of trawl impacts (Blanchard et al., 2009). Community numbers may be linked to functional role, but typically less strongly than biomass
Public awareness	✓. Concept of numbers easily understood and visualized	✓. Concept of biomass easily understood and visualized	✓. Concept of numbers easily understood and visualized
Cost—Largest cost element in all cases is at-sea sampling	×. Relatively high cost as requires identification and counting of all taxa	×. Relatively high cost as requires identification and weights of all taxa	✓. Relatively low cost as requires counting and no identification
Measurement—All benthic sampling reveals high variation in abundance over small spatial scales	✓. Widely recorded (Sciberras et al., 2018). Present results and others show signal can be distinguished from noise and environment (e.g. Atkinson, Field, & Hutchings, 2011)	×. Less widely recorded than numbers (Sciberras et al., 2018). Some results (Link et al., 2005), but not present results, show signal can be distinguished from noise and environment	✓. Widely recorded, present results and others (Sciberras et al., 2018) show signal can be distinguished from noise and environment
Historical data—% of comparative studies from systematic review ($n = 67$) in Hughes et al. (2014)	✓. Available, the majority of existing monitoring and studies have counted and identified fauna (Hiddink et al., 2019; Sciberras et al., 2018). Quantified in 52% of studies here	✓. Some available in existing monitoring and studies that weighed and identified fauna (Hiddink et al., 2019; Sciberras et al., 2018). Quantified in 25% of studies here	✓. Available, the majority of existing monitoring and studies have counted fauna (Hiddink et al., 2017; Sciberras et al., 2018). Quantified in 45% of studies here
Sensitivity	✓. For several taxa (present results)	×. (present results), but ✓ for some species in some studies (Link et al., 2005)	✓. (present results)
Responsiveness—Recovery is slower in highly impacted systems (Hiddink et al., 2017)	✓. For several taxa. Response of numbers faster than biomass (present results) & (Hiddink et al., 2019; Sciberras et al., 2018)	×. Not for present results, but did so for some species in some studies (Link et al., 2005)	✓. Response of numbers is faster than biomass (present results) & (Hiddink et al., 2019; Sciberras et al., 2018)
Specificity	✓. Response to trawling can be disentangled from the effects of other factors (present results)	×. No response to trawling (present results), but did so for some species in some individual studies (Link et al., 2005)	✓. Response to trawling is relatively large and can be disentangled from other factors (present results)

well as numbers, and energy flow through food webs and other ecosystem processes that are linked more closely to biomass. Evenness/dominance and the Shannon–Wiener diversity index are not useful indicators of the impact of trawling as they do not consistently respond to trawling. This explains why compound indices that combine

these diversity indices with other descriptors of the benthic community, such as the Danish Quality Index and Swedish Benthic Quality Index are not responding to trawling (Gislason et al., 2017) and likewise should not be used as state indicators to describe the effects of trawling pressure.

Community biomass	Evenness J'	Shannon–Wiener index H'	Species richness
✓. Directly observable.	✓. Evenness is indirectly estimated from abundance by taxa, but may be directly observable	×. Indirectly estimated from abundance by taxa and is not directly observable	✓. For taxa that are large and conspicuous, and is directly observable (but requiring taxonomic expertise)
✓. Relevant to quantity of biota and links to pressure supported by models of trawl impacts (Allen & Clarke, 2007; Hiddink et al., 2006). Community biomass linked to functional role	×. Meets criterion for relevance to diversity but expected direction of response not obvious or unidirectional. No theoretical models	×. Meets criterion for relevance to diversity but direction of response not obvious or unidirectional. No theoretical models	✓. Relevant to diversity. Strongly affected by the number of individuals in a sample and difficult to separate from community numbers (Gislason et al., 2017). Models not well established (Hiddink et al., 2006). Theory links species richness to functioning (Gamfeldt et al., 2015)
✓. Concept of biomass easily understood and visualized	×. Derived metric whose technical meaning is less easily understood	×. Derived metrics not easily understood	✓. Concept of more or less species in an area easily understood and visualized
✓. Lowest cost as requires weighing of all individuals collectively and no identification	×. High cost as requires identification and counting of taxa	×. High cost as requires identification and counting of taxa	×. Relatively high cost as requires identification of all taxa
✓. Less widely recorded than numbers (Sciberras et al., 2018). Signal can be distinguished from noise and environment (present results, e.g. Hinz, Prieto, & Kaiser, 2009)	×. Not widely calculated. Present results and others (e.g. Goldberg et al., 2012) show signal cannot be distinguished from noise and environment	×. Not widely calculated. Present results and others (e.g. Goldberg et al., 2012) show signal cannot be distinguished from noise and environment	✓. Widely recorded (Sciberras et al., 2018). Present results show signal can be distinguished from noise and environment
✓. Some available, a proportion of existing monitoring and studies have weighed fauna (Hiddink et al., 2017; Sciberras et al., 2018). Quantified in 25% of studies here	✓. Can be derived as most existing monitoring and studies have counted and identified fauna (e.g. Atkinson et al., 2011; Smith, Collie, & Lengyel, 2013). Quantified in 19% of studies here	✓. Can be derived as most existing monitoring and studies have counted and identified fauna (Hannah, Jones, Miller, & Knight, 2010). Quantified in 25% of studies	✓. Can be derived as most existing monitoring and studies have identified fauna. (Sciberras et al., 2018). Quantified in 46% of studies
✓. (present results)	×. (present results)	×. (present results) but effect in individual studies (McConnaughey, Mier, & Dew, 2000)	✓. (present results)
✓. Response of biomass slower than numbers (present results) & (Hiddink et al., 2017)	×. (present results). Response not necessarily unidirectional	×. (present results). Response not necessarily unidirectional	✓. (present results)
✓. Response to trawling can be disentangled from the effects of other factors (present results)	×. No response to trawling (present results)	×. No response to trawling (present results)	✓. Responds to trawling and can be disentangled from other factors (present results). Indicator of richness is confounded by the measures of abundance through the number of individuals sampled)

ACKNOWLEDGEMENTS

The study was funded by the David and Lucile Packard Foundation; the Walton Family Foundation; the Food and Agriculture Organisation of the United Nations; The Alaska Seafood Cooperative; American Seafoods Group U.S.; Blumar Seafoods Denmark; Clearwater

Seafoods; Espersen Group; Glacier Fish Company LLC U.S.; Gorton's Inc.; Independent Fisheries Limited N.Z.; Nippon Suisan (USA), Inc.; Pacific Andes International Holdings, Ltd.; Pesca Chile S.A.; San Arawa, S.A.; Sanford Ltd. N.Z.; Sealord Group Ltd. N.Z.; South African Trawling Association; and Trident Seafoods and the FP7

project BENTHIS (312088). We thank Andrew J. Davies, Mattias Green and Sophie Wilmes (Bangor University) for providing environmental data. Katie Moorhead, Claire Szostek, Kathryn Hughes, Brian Kneafsey and others contributed to data extraction. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect those of NOAA or the Department of Commerce. We thank Rute Pinto, Jake Rice and an anonymous reviewer for constructive comments on this manuscript.

AUTHORS' CONTRIBUTIONS

J.G.H., S.J., M.J.K. and R.H. conceived the ideas and designed methodology; All authors contributed to data-collation; J.G.H. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The systematic review database is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bzkh1895k> (Hiddink et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Hiddink JG, Kaiser MJ, Sciberras M, et al. Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. *J Appl Ecol*. 2020;57:1199–1209. <https://doi.org/10.1111/1365-2664.13617>