

Which ecological indicators can robustly detect effects of fishing?

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Many ecological indicators have been proposed to detect and describe the effects of fishing on marine ecosystems, but few have been evaluated formally. Here, simulation models of two marine systems off southeastern Australia (a large marine embayment, and an EEZ-scale regional marine ecosystem) are used to evaluate the performance of a suite of ecological indicators. The indicators cover species, assemblages, habitats, and ecosystems, including quantities derived from models such as Ecopath. The simulation models, based on the Atlantis framework, incorporate the effects of fishing from several fishing gears, and also the confounding impacts of other broad-scale pressures on the ecosystems (e.g. increased nutrient loads). These models are used to provide fishery-dependent and fishery-independent pseudo-data from which the indicators are calculated. Indicator performance is quantified by the ability to detect and/or predict trends in key variables of interest (“attributes”), the true values of which are known from the simulation models. The performance of each indicator is evaluated across a range of ecological and fishing scenarios. Results suggest that indicators at the community level of organization are the most reliable, and that it is necessary to use a variety of indicators simultaneously to detect the full range of impacts from fishing. Several key functional groups provide a good characterization of ecosystem state, or indicate the cause of broader ecosystem changes in most instances.

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Introduction

The concept of sustainable fishing has evolved over the past two decades to focus increasingly on the wider ecological impacts of fisheries on marine ecosystems (Constable, 2001; Sainsbury and Sumaila, 2003). In Australia, this has led to legislation that requires assessment of fisheries impacts on the environment (including habitats and foodwebs), not just on target species (Environment Australia, 2001). Unfortunately, the legislation requiring such evaluation has developed ahead of the science needed to provide appropriate assessments.

Together with suitably chosen reference points, ecological indicators can serve two purposes in relation to managing the impacts of fishing. First, they can be used to define performance measures to track how well management objectives are being achieved. Second, they can be used as part of decision rules to determine adaptive

management strategies to respond to those impacts. Both uses are common in single-species fishery management, but are yet to be widely adopted in managing the broader ecological impacts of fishing (Sainsbury *et al.*, 2000).

Many ecological indicators have been proposed for use in assessing impacts of fishing, and there have been several recent reviews (Vandermeulen, 1998; Hall, 1999; Murawski, 2000; Rice, 2000; ICES, 2001; Rochet and Trenkel, 2003). Field tests have been used to evaluate a restricted number of indicators (Link *et al.*, 2002; Trenkel and Rochet, 2003; Nicholson and Jennings, 2004), but a formal evaluation of the robustness of many others is still lacking. Robustness in this context refers to the consistency of performance across alternative ecosystem types, levels of perturbation intensity, and sampling uncertainty.

Empirical evaluation of indicator robustness requires large bodies of data from well-studied systems. Computer simulation can provide a cost-effective alternative where

such data are lacking. Although this approach cannot guarantee that the indicators identified are indeed robust, it can provide an efficient screening tool to eliminate those that are unlikely to perform well with real data. An additional benefit of using modelled data is that the analyst is certain about the true properties of the system generating the data, which is a difficulty for real systems, even when they are well studied. We use computer simulations to evaluate a range of potential indicators (including those derived from network theory and existing ecosystem models), using as case studies two marine ecosystems in Australian waters. The simulations take into account aspects of the data collection scheme, including sampling design and the statistical precision of the samples.

Methods

Operating model

In the fisheries context, operating models are caricatures of the real world that seek to incorporate sufficient aspects of the dynamics of real systems to serve as a useful test bed for evaluating management strategies (Butterworth and Punt, 1999; Sainsbury *et al.*, 2000). This approach treats operating models as though they were the real world, “monitoring” them (to generate data), and applying estimation methods and feedback control rules to see if any particular monitoring and regulation strategies consistently produce better results (judged against management objectives) as model parameters are varied (such strategies would be termed “robust”). Most applications of the approach to date have focused on harvest strategies for target species. For testing ecological indicators, the operating model is determined largely by the data it must generate, so that the indicators can be calculated. In this case, the operating model must represent the dynamics of populations, communities, habitats, and entire food chains, including the effects of fishing (and possibly the confounding effects of other anthropogenic pressures). We have chosen the biogeochemical ecosystem-modelling framework “Atlantis” (Fulton *et al.*, 2004b) as the basis for our simulation. This model was parameterized to mimic two contrasting systems: an enclosed temperate marine bay (Port Phillip Bay, near Melbourne, Australia; Bay model), and a large-scale coast-to-open ocean system (the EEZ for much of eastern and southern Australia; EEZ model).

The Atlantis framework, developed from the “Bay Model 2” ecosystem model (Fulton *et al.*, 2004a), is a deterministic model that tracks the nutrient (nitrogen and silica) flow through the main biological groups found in temperate marine ecosystems (Table 1), and three detritus groups (labile detritus, refractory detritus, and carrion). The invertebrate and primary producer groups are simulated using aggregate biomass pools, while the vertebrates are represented through age-structured models. The primary processes considered are consumption, production, waste

Table 1. Biological groups included in the two operating models.

Bay model (29 groups)	EEZ model (39 groups)
Large phytoplankton	Large phytoplankton
Picophytoplankton	Small phytoplankton
Dinoflagellates	Seagrass
Autotrophic flagellates	Macroalgae
Microphytobenthos	Small zooplankton
Seagrass	Mesozooplankton
Macroalgae	Large carnivorous zooplankton
Small zooplankton	Gelatinous zooplankton
Heterotrophic flagellates	Cephalopods
Large omnivorous zooplankton	Pelagic bacteria
Large carnivorous zooplankton	Sedimentary bacteria
Pelagic free bacteria	Meiobenthos
Pelagic attached bacteria	Deposit feeders
Aerobic sediment bacteria	Carnivorous infauna
Anaerobic sediment bacteria	Benthic grazers
Meiobenthos	Deep filter-feeders
Deposit feeders	Shallow filter-feeders
Carnivorous infauna	Deep macrozoobenthos
Benthic grazers	Shallow macrozoobenthos
Benthic filter-feeders	Small planktivorous fish
Macrozoobenthos	Large planktivorous fish
Planktivorous fish	Shallow piscivorous fish
Piscivorous fish	Deep piscivorous fish
Demersal fish	Tropical piscivorous fish (tunas)
Herbivorous demersal fish	Migratory mesopelagic fish
Seabirds	Non-migratory mesopelagics
Shorebirds (waders)	Shallow demersal fish
Sharks	Deep demersal fish
Marine mammals	Flathead (<i>Neoplattycephalus</i> spp.)
	Ling (<i>Genypterus blacodes</i>)
	Orange roughy (<i>Hoplostethus atlanticus</i>)
	Southern bluefin tuna (<i>Thunnus maccoyii</i>)
	Gummy shark (<i>Mustelus antarcticus</i>)
	Demersal sharks
	Pelagic sharks
	Seabirds
	Pinnipeds
	Baleen whales
	Toothed whales

production, migration, predation, recruitment, habitat dependence, and natural and fishing mortality.

Atlantis is spatially resolved, with a polygonal geometry that matches the major geographical features of the system simulated (Figure 1). The size of each polygon reflects the extent of spatial homogeneity in the physical variables represented in the model (depth, seabed type [reef or flat], canyon coverage, porosity, bottom stress, erosion rate, salinity, light, and temperature). Atlantis is also vertically structured. Here we used one sediment layer and up to five water column layers within each box (Figure 1). The

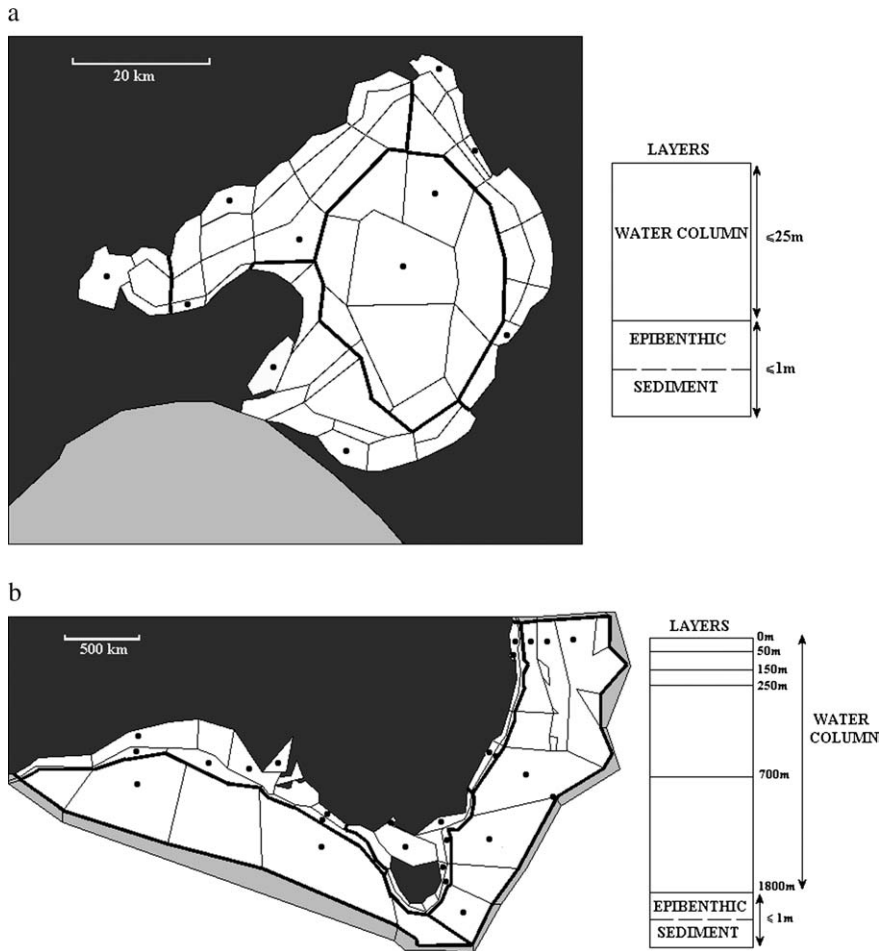


Figure 1. Horizontal and vertical spatial geometries used to define the ecosystems in (a) the Bay model, and (b) the EEZ model (maps: fine lines indicate internal box boundaries, thick lines mark the edges of management zones, and sampling locations are indicated by black dots; vertical stratification: layers are truncated according to the maximum depth of the water column in each box; open ocean cells > 1800 m deep have no epibenthic or sediment layers, and are treated as having an open boundary under the water column).

biological components are replicated in each layer of each box, with movement among boxes and layers dealt with explicitly (allowing for migration of biota of higher trophic levels), or by a transport model (for advective transfer).

The harvesting submodel allows for multiple fleets (eight in the bay model, 25 in the EEZ model), each with its own characteristics (gear selectivity, habitat association, target, by-product [landed and marketed non-target] and bycatch [discarded non-target] groups, effort dynamics, and management structures). While not as sophisticated as fleet-dynamics models of the behaviour of individual vessels (Little *et al.*, 2004), Atlantis does represent the dynamics of aggregate fleets and allows for behavioural responses, such as effort displacement in response to local stock depletion, or the creation of Marine Protected Areas.

While important, aspects of structural uncertainty and parameterization of the model are not dealt with explicitly

here, they have been considered by Fulton (2001) and Fulton *et al.* (2004a, b). The model appears to capture the dynamics observed in real ecosystems, conforms to general ecological checkpoints such as Sheldon spectra (Sheldon *et al.*, 1972), and produces spatial zonation and long-term cycles characteristic of natural systems. The model does have its limitations, however. Although elaboration of the representation of the benthic invertebrate biomass pools has corrected many of the problems identified in earlier versions (Fulton *et al.*, 2004a, b), questions remain about some aspects of infauna dynamics (e.g. speed of response to perturbation). Also, as the model is not eddy-resolving, deep-ocean standing phytoplankton crops are underestimated in some locations. These problems are not critical impediments to the use of Atlantis as an operating model. The more important model limitation to keep in mind here is that, as the base biological rate parameters are fixed

within a run, the model does not currently represent shifts in species composition and biodiversity within biomass pools likely to be associated with the impacts of largely non-selective fisheries (e.g. trawl fisheries).

Sampling model and the scenarios

The sampling model generates data with realistic levels of measurement uncertainty (bias and variance), based on the outputs from the operating model, given specifications for temporal and spatial sampling design, intensity, and precision (for details see [Fulton *et al.*, 2003](#)). For example, fisheries-dependent data can be aggregated over the entire area by quarter, whereas fisheries-independent data (such as surveys or diet composition) may only be available infrequently (annually to once every decade) from “snapshots” taken at specific sampling locations ([Figure 1](#)). The distribution of sampling locations was chosen to mimic the stratified monitoring schemes used in real systems ([Newell and Harris, 1997](#)). The sampling model was run repeatedly for each fishing scenario (30 and 100 times for the EEZ and Bay model, respectively) to reflect uncertainties in the observation and monitoring process.

Four fishing pressure scenarios were developed for both case studies: (i) no fishing, (ii) moderate exploitation, (iii) heavy exploitation, and (iv) simultaneous impacts of different anthropogenic activities (fishing, nutrient load, and habitat degradation). The scenarios spanned 90 years for the Bay model and 120 years for the EEZ model, and include staggered starts for different fleets – fisheries targeting lower trophic levels or stocks in areas that are harder to access (e.g. deep water) only commence once catch rates for easily accessible stocks of higher trophic levels dip (either locally or over the entire area). This reflects the tendency to deplete ecosystems sequentially by “fishing down the foodweb” ([Pauly *et al.*, 1998](#)).

Indicator and attribute analyses

Close to 100 different types of indicator were identified in the literature review by [Fulton *et al.* \(2004b\)](#). We considered only a subset of these, all of which are univariate. The specific types considered ([Table 2](#)) were selected because they either show promise because of their relative clarity, sensitivity, exclusiveness, or measurability, or have been used widely (e.g. diversity indices), or have given promising results in recent fieldwork (e.g. maximum length in the catch; [Miller and Cury, 2003](#)).

Indicator values were calculated with the model-generated data, after pooling across sampling locations into user-defined monitoring or management zones. An Ecopath model was created, using the sampled data together with simple decision rules for achieving a balanced model, to calculate those indicators that are network- or model-dependent. Model mis-specification can and did arise in the Ecopath model, owing to sampling

variability in data inputs for both biomass and diet data. For instance, groups that are hard to sample, have small biomass pools, or migrate seasonally, may be missed by the sampling and so would be omitted. Similarly, rare dietary items may be missed during the collection of diet data, so the associated links would be omitted from the Ecopath model.

Indicator performance was assessed by their ability to track properties of interest (attributes). These attributes largely reflect ecosystem- and community-level properties that span the major ecological structures and processes of public and legislative concern ([Punt *et al.* 2001](#)). The ecosystem characteristics that are most visible and readily identified by interested sectors of society (“what and how much is there?” and “who eats who?”) are represented by the following attributes: biomass, diversity, size structure, spatial structure, foodweb structure, trophic level, and the number of groups representing 80% of the biomass. The remaining community- and ecosystem-level attributes deal with flows and ecosystem functioning. Throughput, consumption, and production reflect a system’s ability to support its current state (and any exploitation) in the long term. Nutrient-cycling attributes (size of nutrient pools, rates of nitrification and denitrification, and the ratio of labile to refractory detritus) capture this too, along with the internal state of the ecosystem and its flows. These attributes are the focus in water quality monitoring, because of the widely recognized detrimental effects associated with eutrophication ([Rappart, 1992](#); [Harris *et al.*, 1996](#)). Lastly, respiration (particularly relative to production) captures the overall state or maturity of an ecosystem ([Christensen, 1992](#)). This is important ecologically, but also socially because, at a gross level, people tend to find mature systems more aesthetically pleasing because they often contain more internalized flows, more specialization, and more diverse biota ([Odum, 1969, 1997](#); [Schneider and Kay, 1994](#)). While this is a strong generalization of the complex and somewhat controversial concept of ecosystem maturity, the use of a maturity attribute is important, as reflected by its inclusion in many “ecosystem health” studies ([Müller and Maren, 1998](#); [Casselman *et al.*, 1999](#); [Johnson *et al.*, 2001](#)).

The ability of indicators to mimic the attributes correctly was assessed by plotting each indicator against each attribute and examining the correlation. To check for sensitivity of the results to fishing intensity, level of data aggregation, and statistical assumptions of the methods used, the analyses were repeated using Pearson and Spearman correlation for each scenario, at two levels of spatial aggregation (by management zone, and over the entire area; [Figure 1](#)). Thus, for each indicator, 208 correlations of each type (Pearson and Spearman) were performed for the Bay model (two degrees of data aggregation, by four fishing scenarios, by 26 attributes), and 288 for the EEZ model (2 by 4 by 36). Indicator performance is then rated to identify robust ones – those

Table 2. Types of indicators evaluated (Ph, physical; P, population level; C, community level; E, ecosystem level; *, model-dependent or relying on knowledge of a network structure; B, biomass/stock size; Φ , trophic level).

Indicator	Indicator type	Reference
Average Φ *	C, E	Greenstreet and Hall (1996); Rochet and Trenkel (2003)
B – relative to unexploited level (or other baseline); by community and by group	C, P	Murawski (2000)
Capacity*, overhead*, and relative ascendancy*	C, E	Ulanowicz and Abarca-Arenas (1997); Christensen <i>et al.</i> (2000)
Chlorophyll <i>a</i>	Ph	Monbet (1992)
Condition at maturity (c_m) or size at maturity (s_m)	P	ICES (2001)
cpue – by community and by group	C, P	Jennings <i>et al.</i> (2001)
Coefficient of variation (CV_t) of B	E	Blanchard and Boucher (2001)
Detrital dominance*	E	Christensen <i>et al.</i> (2000)
Discard rate – total, by community, and by group	C, P	Jennings <i>et al.</i> (2001)
Dissolved Inorganic Nitrogen (DIN)	Ph	Monbet (1992)
Diversity – species richness/count of groups present (Div)	C, E	Rice (2000); Rochet and Trenkel (2003)
Ecotrophic efficiency* (EE) – across a set of groups and by group	C, P	Christensen <i>et al.</i> (2000)
Fishing in balance* (FIB) – using Φ fixed at starting values and updated diet data	E	Pauly <i>et al.</i> (2000)
Infaua:epifauna biomass ratio (InF:EpF)	C	Fulton <i>et al.</i> (2003)
Labile:refractory detritus biomass ratio (LabD:RefD)	C, E	Fulton <i>et al.</i> (2003)
Light levels at sediment surface	Ph	Fulton <i>et al.</i> (2003)
Maximum length in the catch (L_{max})	C	Jennings and Kaiser (1998); Frid <i>et al.</i> (2000); Rochet and Trenkel (2003)
Net primary production/B (NPP/B)	E	Christensen <i>et al.</i> (2000)
Number of charismatic animals caught (#C)	P	Fulton <i>et al.</i> (2003)
Potential biological removals (PBR) – relative to actual catch for mammals and seabirds	P	Wade (1998)
Pelagic:demersal fish B-ratio (PelB:DemB)	C	Caddy (2000); Fulton <i>et al.</i> (2003)
Primary production required* (PPR) and efficiency* – overall and by groups	E, P	Christensen <i>et al.</i> (2000)
Proportion of the stock that are juveniles (JuvP) – by community and by group	C, P	Hilborn and Walters (1992)
Piscivorous:zooplanktivorous fish B-ratio (PvB:ZvB)	C	Caddy and Garibaldi (2000)
Rate of denitrification and nitrification	Ph	Fulton <i>et al.</i> (2003)
Reproductive success – charismatic groups (RS)	P	Goni (1998)
System omnivory index (SOI)*	E	Christensen <i>et al.</i> (2000)
Total mortality (P/B) – by community and group	C, P	Christensen <i>et al.</i> (2000)
Network indices* (production, consumption, respiration, flow to detritus, system exports) – total values for ecosystem, and by group	C, E, P	Christensen <i>et al.</i> (2000)
Total system throughput*	E	Ulanowicz (1986); Christensen <i>et al.</i> (2000)
Trophic efficiency (production and detritus)*	E	Christensen <i>et al.</i> (2000)

that reliably and consistently predict trends in one or more key attributes. The ratings were based on: (i) consistency of the correlations across scales of data aggregation, scenario, and ecosystem type (“Consistent” or “Inconsistent”); (ii) the fraction of attributes for which the absolute value of the correlation coefficient was ≥ 0.5 (“Broad” if $>40\%$, “Restricted” otherwise); and (iii) the absolute value of the correlation coefficients (very clear, $|r| \geq 0.9$; strong, $0.9 > |r| \geq 0.7$; recognizable, $0.7 > |r| > 0.5$; uninformative, non-linear or $|r| \leq 0.5$) for $\geq 85\%$ of the correlations.

This use of correlation coefficients was meant to capture the ease of interpretation of indicator values if applied in reality. The large number of data points involved in each analysis meant that even bi-plots with fairly flat indicator-attribute relationships had statistically significant correlation coefficients. Therefore, significance could not be relied on as a performance measure because, for use in management, only those with a clear linear relationship to attributes are of real practical utility (otherwise it would be too difficult to determine the position on the attribute axis

given the indicator value). Therefore, the absolute value of the correlation coefficient was chosen as the performance measure used to rank the indicators.

Results

Model behaviour

While not reported in detail here, the dynamic behaviour of the attributes for both models show that Atlantis does reproduce behaviour typical of the changes seen in actual exploited ecosystems (Fulton *et al.*, 2004b). Average size of fish decreased by up to 75% under increasing fishing pressure, because of the combined effects of depletion of older age classes of most fish groups, and the reduced abundance of those groups with large adult body sizes (e.g. piscivores). Intensive fishing pressure may also lead to large-scale restructuring of the communities. For example, large demersal sharks were extirpated, while the biomasses of fast-growing cephalopods, gelatinous zooplankton, and small pelagic fish increased substantially. However, forage fish and invertebrates are usually not released from predation until many of their predators have been depleted. The model also predicts a decline in the biomass of habitat-defining epibenthic groups (such as seagrass and filter-feeders). In contrast, there is a concomitant increase in those groups (e.g. deposit feeders) that scavenge carrion (or detritus), or benefit from discarding in other ways. This restructuring of communities does lead to shifts in nutrient cycling and primary production, but the effect is not of universal strength: while some subsystems show a marked shift in primary productivity, the effect is negligible in other subsystems.

Correlation analysis

It is not possible here to present the complete results of the correlation analysis. Instead, a brief summary of the major patterns in the results is provided below along with a table (Table 3) that summarizes the overall performance of the indicators. Readers interested in more detailed results may refer to Fulton *et al.* (2004b).

Although the strength of the linear correlations among indicators and attributes varied with the method used (Pearson or Spearman), results from the two methods were generally consistent. In <10% of all cases (across indicators, system-types, scenarios, and degree of data aggregation), one method identified an indicator-attribute relationship with $|r| > 0.5$ when the other did not. There was no consistent pattern in these differences (i.e. they were not all in the same scenario or model), except that $|r|$ was always < 0.7 .

The strongest and most consistent signal was the pattern of correlations under the various fishing pressure scenarios. With no fishing, 60% and 88% of the indicators for the EEZ and Bay model, respectively, were correlated with more

attributes when data were aggregated to zones, rather than when aggregated across the entire system. In the Atlantis framework, there is allowance for considerable spatial and temporal variation in attributes, particularly for groups with fast turnover rates. Analysis using zones maximizes the spatial contrast in attributes. Compared with the unfished system, fishing greatly reduced the spatial contrasts in the system, and only 32% and 26%, respectively, were correlated with more attributes when data were aggregated to zones.

Table 3 categorizes the indicators by their performance in the correlation analyses. Many of the indicators listed in Tables 2 and 3 correspond directly, but others in Table 3 are more specific. Where the same indicator applied to individual groups performed similarly, the general result is given in Table 3, rather than exhaustively listing each indicator/group combination. Similarly, where the dynamics of a few key groups (discussed below) apparently characterized ecosystem state, the indicators based on those groups are also referred to generally, rather than spelling out each group. Examination of bi-plots (and especially outlier points) as part of the analysis showed that a number of (mostly model-dependent) indicators performed quite differently if sampling and/or estimation errors were higher, or if there was a mis-specification between any assumed network structure, or fishing history, and the actual ecosystem structure or history. If this is the case, two entries are given, one for “good data” and one for “bad data”.

A clear pattern of indicator performance emerges (Table 3). The majority in the categories “Consistent” and “Broad” (41 of 68, and 15 of 21, respectively) were community- or ecosystem-level indicators. In addition, the majority in the category with $|r| > 0.7$ (40 of 65) were also community- or ecosystem-level indicators, whereas all but one of those that were uninformative were population-level or model-dependent indicators. Among the 24 categorized as “Inconsistent”, the ecosystem-level indicators were usually only correlated with attributes when data were aggregated at the system level. In contrast, the “Inconsistent” community- and population-level indicators did not perform consistently better at either level of data aggregation.

Seven indicators were correlated with attributes in only one of the two models. The majority of these appear to be sensitive to whether the system is open or closed. For instance, the proportion of juvenile fish (by number) and the reproductive success of mammals and seabirds are only responsive when dealing with closed populations. These indicators are therefore not informative if there is a non-negligible flow of recruits into the model area from stocks outside.

No indicator was correlated ($|r| > 0.5$) with the entire set of attributes. “Condition-at-maturity of top predators” for the EEZ model performed best with a score of 60–95% across the various scenarios and levels of data aggregation.

Table 3. Classification of (a) indicators performing consistently among aggregation levels and the two models, and (b) those that did not, both based on Pearson and Spearman rank correlations between indicators and ecosystem attributes for the four fishing pressure scenarios, two data aggregation levels and two models (B, biomass; D, Discards; Φ , trophic level; Z, total mortality; good and poor refer to data quality where this made a difference; see text for further explanation).

Correlations (>85%)	Broad (>40% with $ r > 0.5$)	Restricted (<40% with $ r > 0.5$)
<i>a. Consistent performance (across models and level of aggregation)</i>		
Very clear ($ r \geq 0.9$)	Average Φ (good) B – detritus/sharks/target groups c_m/s_m – top predators PelB:DemB Total benthic production Total B	Average Φ indicator groups (good) B – planktivores c_m/s_m – seabirds/target groups Detritus (B-ratio) L_{max} PS/ZP (B-ratio) Total primary production
Strong ($0.9 > r \geq 0.7$)	B – epifauna/gelatinous zooplankton cpue – demersal fish EE – overall (good) PPR – catch (good)/overall (good) Total consumption (good) Total production (good) Total respiration (good)	Average F vertebrates (good) B – infauna/mammals/seabirds/seagrass* Capacity (good) Chl a^* cpue – epifauna/piscivores/planktivores/sharks CV_t Detrital dominance (good) D – demersal fish/invertebrates/piscivores/ planktivores (all good) Div DIN* Efficiency of catch – demersal fish (good) FIB PBR – mammals PelB:DemB – catch PvB:ZvB – catch SOI Total catch (good) Total throughput (good)
Recognizable ($0.7 > r > 0.5$)	PPR – catch (poor) JuvP – catch Total consumption (poor) Total infauna consumption Total production (poor)	Average Φ (poor)/individual groups (poor) B – bacteria/plankton cpue – mid- Φ groups Denitrification EE – individual groups (good) Nitrification #C mammals PPR – overall (poor)/individual groups (good) Total flow to detritus Total zooplankton production Z – demersal fish/mammals/piscivores/sharks
None ($0.5 > r $)	Average F catch (fixed) (poor)/vertebrates (fixed) (poor) B – individual non-indicator groups (particularly microfauna/microflora) Capacity (poor) cpue – low- Φ groups/individual groups (if non-linearly related to abundance) c_m/s_m – non-target small-bodied groups Consumption – individual groups Detrital dominance (poor) D – demersal fish (poor)/invertebrates (poor)/piscivores (poor)/planktivores (poor)/ individual groups (particularly those with high growth rates) EE – overall (poor)/individual groups (poor)	

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Table 3 (continued)

Correlations (>85%)	Broad (>40% with $ r > 0.5$)	Restricted (<40% with $ r > 0.5$)
<i>b. Inconsistent performance (across models and level of aggregation; letters in parentheses specify under what circumstances indicators did correlate with ecosystem attributes: z – data aggregated by management zone; s – data aggregated to system level; b – Bay model only; o – EEZ model only).</i>		
Very clear ($ r \geq 0.9$)	Total D rate (s-good)	Average Φ catch (z-good) B – cephalopods (z)
Strong ($0.9 > r \geq 0.7$)		Average F catch (fixed) (z-good) B – macroalgae (z) cpue – cephalopods (z) Efficiency of catch – piscivores (o-good) FIB (fixed F) (z) InF:EpF (m) PBR – seabirds (s) JuvP fish stock (o) Trophic efficiency – detritus (o-good)/production (z-good)
Recognizable ($0.7 > r > 0.5$)	Z – filter-feeders (z)	Average Φ of catch (z-poor) Light at sediment surface (z) NPP/B (good) (b) #C seabirds (b) Overhead (z-good) Relative ascendancy (s-good) RS – seabirds (b)/mammals (b,z) Z – macrozoobenthos (m)/planktivores (s)/seabirds (z)
None ($0.5 > r $)	Efficiency of catch – demersal fish (poor)/piscivores (poor) NPP/B (poor) Overhead (poor) PPR – individual groups (poor) Production – individual microfauna/microflora groups Relative ascendancy (poor) Total catch (poor) Total D rate (poor) Z – individual non-indicator groups (particularly microfauna/microflora) Total respiration (poor) Total throughput (poor) Trophic efficiency – detritus (poor)/production (poor)	

*These are good ancillary indicators for checking for additional effects of eutrophication.

This is substantially higher than the overall average of only 17.5% (and may be an artefact of model formulation; size at maturity also performed well and may be a more reliable indicator in reality). The skewed distribution of attribute-indicator correlations meant that some attributes were not correlated with many indicators. Across the scenarios and levels of data aggregation, approximately 60–75% of the correlations involved biomass-related attributes, size-structure attributes, trophic-level or foodweb structure. The remaining ecosystem-level and flow attributes (respiration, production, nutrient cycling, throughput) were relatively poorly represented in the correlations, involving only 6–30% of the correlations. Across the scenarios in both models, community- and ecosystem-level indicators (such

as biomass ratio of pelagic: demersal fish, or the CV of total biomass) were three times more likely than population-level indicators to be correlated with at least 50% of the attributes.

Discussion

Selection of appropriate indicators

Table 3 identifies a subset of indicators that not only are capable of tracking changes in a broad set of attributes, but whose interpretation is robust to ecosystem type, exploitation pattern, and/or level of data aggregation. At the other extreme, many indicators are only weakly correlated with

a restricted number of attributes, and then only under certain circumstances.

The simulation results confirm the expectation that no single indicator (or type) provides a complete picture of ecosystem state. Rather, a suite of indicators will be required, each focusing on different attributes, using different kinds of data, and spanning groups and processes with fast and slow dynamics. The main biological groups that need to be included are:

- (i) groups with fast turnover rates (e.g. phytoplankton, zooplankton, bacteria) that, while non-selective (they do not only respond to fisheries-induced perturbations), will nevertheless respond quickly to any change in the system (such groups may cause false alerts, but react sufficiently fast to be potentially useful as early warning indicators);
- (ii) groups that are targeted by fisheries (they can usefully summarize the current status of that part of the foodweb of most interest to humans);
- (iii) habitat-defining groups (particularly in coastal ecosystems, because they have critical roles in benthic communities and are often a good proxy for overall biodiversity levels);
- (iv) charismatic (or sensitive) groups (often found at the top of the foodweb, such groups usually have slow dynamics and can convey information about the underlying system state, and how heavily it has been impacted by fishing).

Use of a suite of carefully selected indicator groups from these categories should achieve a reasonable balance of early signal detection and system characterization. Such a suite should guard against false signals, because it should capture a greater range of attributes, and be less likely to suffer simultaneously from data error and system dependences.

With regard to overall performance and robustness, community- and ecosystem-level indicators were usually the most informative (Tables 3). This is perhaps not surprising given that most attributes are also community- and ecosystem-level properties. Table 4 summarizes the results in terms of guidelines for the selection of indicators that most effectively capture ecosystem dynamics, based on the simulations presented. Although a few population-level indicators appear to perform quite well and feature in this list, even those often refer to specific groups rather than to a random selection. Overall, population-level indicators evaluated appear to be too sensitive to short-term fluctuations or to other species-specific factors to be effective indicators for integrated community- and ecosystem-level attributes.

Indicator responsiveness, the speed with which it signals a change in the ecosystem, is important in a management context. Once this factor is taken into account, community-level indicators appear to be an effective compromise among data requirements, signal strength, and sensitivity to

Table 4. Guidelines for selecting univariate indicator(s) that most effectively capture the dynamics of each attribute (P, population; C, community; E, ecosystem); indicators are more effective is using the indicator groups identified in the discussion rather than just any groups.

Attribute (type)	Univariate indicator(s)
Biomass (P, C, E)	B by group (P) or community (C)
Consumption (C, E)	Estimated consumption by group (P) or community (C, E)
Diversity – species, group, flow (C, E)	Simple (transparent) diversity indices (E)
Foodweb structure (E)	Lacking good diet data, indicators used for size structure (C) and Φ (E) also give insight
# groups to represent 80% of B (C, E)	B by group (P) or community (C)
Nutrient cycling (E)	Estimated denitrification (E; particularly for shallow-water ecosystems), DIN (E), and network total production (E), if good data available
Production (P, C, E)	Estimated production by group (P) or community (C); total primary production (E)
Respiration (C, E)	If good diet data and knowledge of ecosystem structure, use estimated respiration or total production (E) from network models (E), otherwise use total production by group (P); in shallow-water systems, denitrification (E) also useful.
Size structure (P, C)	B-ratios (e.g. P _v B:Z _v B, P _{el} B:DemB, large:small plankton, InF:EpF) (C), c_m/s_m (P), and L_{max} catch (C)
Spatial structure of B (P, C)	Best derived by mapping biomass indicators (C, P)
Throughput (E)	Estimated using network model (E); estimated total production, consumption, respiration provide good alternatives (E), if have good diet data and knowledge of ecosystem structure.
Trophic level Φ (E)	Average Φ (E) if (and only if) good diet data available; alternatively, size-based indicators (C) are easily collected, and less error-prone

natural variability. This agrees with empirical findings from monitoring studies of water quality (Frost *et al.*, 1992). Community-level indicators respond quickly enough to be of use in management, but are sufficiently aggregated measures to adequately encapsulate fundamental information about system state, and are not particularly sensitive to short-term variations. Unfortunately, recent field studies indicate that careful thought needs to be given to the power of the monitoring schemes employed to detect temporal trends (especially in heavily impacted areas) when using community-level indicators (Nicholson and Jennings, 2004). Further simulation studies may provide a basis for evaluating such power. Moreover, future work with alternative models (and in real-world systems) is needed to verify the results from Atlantis, and to investigate the impact of system details the model does not reproduce well, or does not represent at all (e.g. biodiversity).

Comparisons with previous studies

In general, the relative performance of the various indicators in the simulations supports previous conclusions about their potential usefulness, based on field and small-scale experimental trials. Indicators that use easily sampled data and require few calculation steps (e.g. biomass ratios) had intermediate to strong correlations with many attributes. Of those, biomass and size at maturity have both been proposed because they require relatively few data, and perform consistently regardless of the level of exploitation intensity and the structure of the underlying ecosystem (Jennings *et al.*, 1999; Murawski, 2000; ICES, 2001; Rochet and Trenkel, 2003). Similarly, the indicators that showed potential here, but were sensitive to data quality (such as average trophic level), are recognized as attractive (Jennings *et al.*, 2001). However, debate over the best means of calculating them continues in an effort to minimize data requirements (Rochet and Trenkel, 2003). The performance of general classes of indicators (population- vs. community- vs. ecosystem level) for marine ecosystem monitoring also appears to be consistent with reported performance in other fields of ecosystem monitoring (Frost *et al.*, 1992).

The largest discrepancy with previous results refers to network and model-dependent indicators. Indicators such as relative ascendancy are often proposed in the (theoretical) literature as useful summaries of system state or system dynamics, because they are commensurate with ecosystem properties such as trends in species richness, resource internalization, trophic specialization, and succession (Christensen, 1994; Ulanowicz and Abarca-Arenas, 1997). However, their dependence on data that are difficult to collect, model formulation, and a good knowledge of ecosystem structure, means that their performance is often poor. Although such models and types of indicators may have value in well-studied and data-rich systems, it would be unwise to construct a monitoring system that relied solely, or even heavily, on such indicators.

In this analysis, we did not consider multivariate indicators. Preliminary analyses indicate that, for instance, biomass size spectra, dominance curves, and species-area curves provide good measures of overall system state, by simultaneously providing information on different attributes (biomass, diversity, size structure, trophic level, and production; Fulton *et al.*, 2004b). It has also been shown that some multivariate indicators can be usefully reduced to univariate measures (e.g. using the slope of a size or trophic spectrum; Nicholson and Jennings, 2004; Fulton *et al.*, 2004b).

Ultimately, indicators need to be linked to reference levels that, if exceeded, trigger management actions. So far, it has proven difficult to specify reference levels for any ecosystem indicator, for example, because of difficulties in generalizing across ecosystems (ICES, 2001). However, specifying reference points for single-species fisheries management can also be difficult and controversial (Hilborn, 1997). A promising approach for extending the idea of reference points to cover ecosystems has been put forward by Link *et al.* (2002), who used a principal components analysis to integrate the information from a wide range of indicators. The plotted scores for the first two principal components through time provide a clear map of changes in system state that immediately lends itself to defining reference limits (or areas), and objectives. This approach may not be suited to all ecosystem types, and it may need to be used in unison with concepts such as “best practice” reference points (Sainsbury and Sumaila, 2003). Either way, the development of reference points for ecological indicators would be greatly simplified if some straightforward means of summarizing time-trends from a suite of indicators could be found. Once such a method has been found, the greater issue of the development and testing of adaptive management frameworks that incorporate ecological indicators into the decision rules remains to be completed.

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