A method for identifying keystone species in food web models

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ABSTRACT

Keystones are defined as relatively low biomass species with a structuring role in their food webs. Thus, identifying keystone species in a given ecosystem may be formulated as: (1) estimating the impact on the different elements of an ecosystem resulting from a small change to the biomass of the species to be evaluated for its 'keystoneness'; and (2) deciding on the keystoneness of a given species as a function of both the impact estimated in (1) and its own biomass. Experimental quantification of interaction strength necessarily focus on few species, and require a priori assumptions on the importance of the interactions, which can bias the identification of keystone species. Moreover, empirical measurements, although very important, are expensive and time consuming and, owing to the spatio-temporal heterogeneity of habitats, physical conditions, and densities of organisms, published results tend to be case-specific and context-dependent.

Although models can only represent but a caricature of the complexity of the real world, the modelling approach can be helpful since it allows overcoming some of the difficulties mentioned. Here we present an approach for estimating the keystoneness of the functional groups (species or group of species) of food web models. Network mixed trophic impact analysis, based on Leontief's economic input–output analysis, allows to express the relative change of biomasses in the food web that would result from an infinitesimal increase of the biomass of the observed group, thus identifying its total impact. The analysis of the mixed trophic impacts presented here was applied to a suite of mass-balance models, and the results allow us to rank functional groups by their keystoneness. Overall, we concluded that the straightforward methodology proposed here and the broad use of Ecopath with Ecosim (where mixed trophic impact analysis is implemented) together give a solid empirical basis for identification of keystone functional groups.

1. Introduction

Keystones are defined as species with a structuring role within ecosystems and the food webs that interconnect in spite of a relatively low biomass and hence food intake (Power et al., 1996). It may be noted that the low biomass requirement eliminates species that structure ecosystems by virtue of their high biomass, such as

trees in terrestrial forests, or seagrass and kelp in coastal ecosystems.

Keystone species affect the communities of which they are part in a manner disproportionate to their abundance (Power et al., 1996). Keystone species strongly influence the abundances of other species and the ecosystem dynamic (Piraino et al., 2002). Therefore, it is important to identify keystone species, notably to maintain ecosystem integrity, and biological diversity in the face of exploitation and other stresses (Naeem and Li, 1997; Tilman, 2000). However, it is expected that all species of a given ecosystem rank in a *continuum* of levels of 'keystoneness', with only some designated to be keystone species.

Identifying keystone species in a given ecosystem may be thus formulated as

1. Estimating the interaction strength as the impact on the different elements of an ecosystem resulting from a small change to the biomass of the species to be evaluated for its keystoneness.
2. Deciding on the keystoneness value of a given species as a function of the impact estimated in (1) and its biomass.

Several studies report on field-based, experimental quantification of interactions strength, as evaluated through the impacts induced by changes in abundance of one species on the other species in a community (Paine, 1992; Wootton, 1994; Wootton et al., 1996; Berlow, 1999). However, these experiments necessarily focused on few species; thus, they required a priori assumptions on the importance of the interactions, in order to exclude the uninteresting species from the experiment, which can bias the identification of keystone species (Wootton, 1994; Bustamante et al., 1995).

Although the importance of indirect interactions is recognized (Wootton, 1993, 1994; Yodzis, 2001), their explicit consideration within a purely experimental approach is difficult. Most indirect interactions are weak, which seemingly justifies their being neglected. However, indirect interactions can also be magnified by cascading effects (Brett and Goldman, 1996; Pace et al., 1999), and thus need to be taken into account.

Moreover, empirical measurements of interaction strengths are usually limited to easily accessible, sessile or errant macrobenthic species (Paine, 1992, 2002; Wootton, 1994; Wootton et al., 1996; Berlow, 1999), or microscopic species (Naeem and Li, 1997), because these are easier to manipulate and control than nektonic species (especially large fish, or marine mammals), for which only indirect evidence is available (Power et al., 1996).

Finally, empirical measurements, although very important, are expensive and time consuming (Ernest and Brown, 2001). Consequently, and owing to the spatio-temporal heterogeneity of habitats, physical conditions, and densities of organisms (Paine, 1994, 2002; Piraino et al., 2002), published results tend to be case-specific and context-dependent (Power et al., 1996).

The modelling approach allows overcoming some of the difficulties of the experimental quantification of keystoneness. Through a model it is possible to estimate the strength of the interactions between model functional groups (here referred to as 'species', although often composed of groups of species with similar sizes and feeding habits). Therefore, the modelling approach provides at least a pre-screening analysis and allows for improved planning of subsequent field experiments.

This suggestion is not new. Previous estimates of keystone species from mathematical models exists, based on successive elimination of functional groups from a trophic web and evaluating impacts on the other functional groups using a graph theoretical method (Jordan et al., 1999; Jordan, 2001; Solé and Montoya, 2001), or evaluating changes in the biomass of ecosystem with dynamic models (Okey et al., 2004a).

However, estimating the trophic impact on the functional groups of an ecosystem resulting from a change (increase) of the biomass of a single group can be achieved more directly and rigorously through the mixed trophic impact matrix, **M**, as adopted for food webs by Hannon (1973) from input–output analysis of Leontief (1951). Each element of the matrix represents the relative change of biomass that would result from an infinitesimal increase of the biomass of the functional groups in the rows (Ulanowicz and Puccia, 1990). Thus, **M** can be used to estimate the total effect of one functional group on all the others in a given model.

The analysis of the mixed trophic impacts presented here was applied to a suite of mass-balance models built with the software package Ecopath with Ecosim (http://www.ecopath.org; Christensen and Walters, 2004), allowing the estimation of keystoneness for the functional groups of models representing marine ecosystems spread over the world. The results allow us to rank groups by their keystoneness, which then can be compared with ranking from previous studies, and with the ecological experience resulting from previous experimental research.

Also, the use of models constructed using the same approach, i.e., using Ecopath with Ecosim, allows standardizing the evaluation of species' roles and the quantification of the interaction strengths in various environments, thus providing at least some of the pre-screening alluded to above, and required for the design of experimental studies.

The present paper aims to answer the following questions:

(1) How can we use the matrix **M** obtained for mass-balance models to quantify the total impact of one functional group on the others in the ecosystem?
(2) Do the resulting estimates obtained in this manner make ecological sense?
(3) How do we ensure that our measure of keystoneness correctly balances the strength of interactions measured through the total effects (by and on species) and the effect that species exert due to their biomass?
(4) What are, in general, the major features of keystone species identified in a comparative analysis of models representing different ecosystems?

2. Methods

2.1. *Ecopath approach*

Ecopath is the core routine of the Ecopath with Ecosim (EwE), a software package based on an approach proposed by Polovina (1984) and subsequently upgraded with a variety of ecologi-

cal and theoretical approaches (Christensen and Pauly, 1992; Walters et al., 1997, 2000; Pauly et al., 2000; Christensen and Walters, 2004). Ecopath allows construction of a mass-balance model of a given trophic network by representing the ecosystem functional groups as interacting by means of feeding relationships and, when necessary, subjected to fishing (Christensen and Walters, 2004). The balance of mass (energy, or nutrients) for any functional group (i) of the network is obtained by setting its production equal to the sum of the consumption components, expressed as

$$\left(\frac{P}{B}\right)_i B_i = \sum_{j=1}^{n} \left(\frac{Q}{B}\right)_j B_j DC_{ij} + E_i + Y_i + BA_i + \left(\frac{P}{B}\right)_i B_i (1 - EE_i)$$

$$(1)$$

where production, on the left side of the equation, is expressed as the product between the production–biomass ratio (P/B_i) and the biomass (B_i), and the right-hand side terms are the sum of the predation terms, each expressed as the product of the consumption–biomass ratio (Q/B_j), the biomass of the predators (B_j) and the proportion of the prey i in the diet of the predator j (DC_{ij}); the net flow trough the boundaries of the system, i.e., dispersal (E_i); the fishing exploitation, represented through the catches (Y_i); the accumulation or depletion of biomass (BA_i); and non-predation natural mortality, expressed by means of the ecotrophic efficiency (EE_i). The resulting system of equations, when solved, provides a snapshot of the flows within a trophic web (numerous examples are reported in Christensen and Pauly, 1993; see also http://www.ecopath.org).

2.2. Mixed trophic impact

Given the mass-balance model of a trophic network, the mixed trophic impact is estimated for each pair of functional groups (i, j, interacting directly or not) of the trophic web, by means of the net impact matrix. According to Ulanowicz and Puccia (1990), the net impact of i on j (q_{ij}) is given by the difference between positive effects, quantified by the fraction of the prey i in the diet of the predator j (d_{ji}), and negative effects, evaluated through the fraction of total consumption of i used by predator j (f_{ij}). Therefore the resulting matrix of the net impacts, $\mathbf{Q}$, has elements:

$$q_{ij} = d_{ji} - f_{ij} \qquad (2)$$

The mixed trophic impact m_{ij} is then estimated by the product of all the net impacts q_{ij} for all the possible pathways in the trophic web that link the functional groups i and j. Ulanowicz and Puccia (1990) demonstrated that the matrix of the mixed trophic impacts, $\mathbf{M}$, can be obtained by the inverse of the matrix $\mathbf{Q}$, as it is calculated in EwE (Christensen et al., 2004). Table 1 shows the elements of such matrix $\mathbf{M}$ derived from a food web representing the ecosystem off the coast of Newfoundland (Bundy, 2001).

The elements m_{ij} of the matrix $\mathbf{M}$ quantify the direct and indirect impacts that each (impacting) group i has on any (impacted) group j of the food web (Ulanowicz and Puccia, 1990). Positive/negative values of m_{ij} indicate the

increase/decrease of biomass of the group j due to a slight increase of biomass of the impacting group i. Thus, the mixed trophic impacts represent the first order partial derivatives, in term of biomass, of the Ecopath master equation (1). This can be illustrated by Ecosim simulations, as shown below.

Moreover, from Eq. (2) one can tell that negative elements of matrix $\mathbf{M}$ indicate a prevailing of negative effects, i.e. the effects of the predator on the prey; analogously, positive elements of $\mathbf{M}$ indicate prevailing effects of the prey on the predator. Therefore, negative elements of $\mathbf{M}$ can be associated to prevailing top-down effects and positive ones to bottom-up effects.

2.3. Ecosim

The dynamic routine of the EwE package, Ecosim, is based on a set of differential equations, derived from the Ecopath's master equation (1), allowing dynamic representation of the system variables, i.e. biomasses, predation, and production (Christensen and Walters, 2004). In order to describe dynamically the predator–prey interaction, Ecosim uses Lotka–Volterra relationships modified to account for foraging arena theory (Walters et al., 1997, 2000), which allow to avoid the unrealistic Lotka–Volterra assumption of uniform and random distribution of interactions, typically assumed with the mass-action functions (Walters and Martell, 2004). In foraging arena theory, rather, the biomass of the prey available to predators is only a vulnerable fraction of total biomass, with exchanges rates between the vulnerable and the invulnerable states calculated using vulnerability coefficients set by the user (Christensen and Walters, 2004).

2.4. Comparison between simulation outputs and matrix M

In order to test if the elements of $\mathbf{M}$ represent the relative change of biomass that would result from an infinitesimal increase of the biomass of the functional groups in the rows, a set of Ecosim simulations (covering a period of 100 years) were done. Since biomass and production are multiplicative terms in EwE formulations, changing proportionally one or the other has identical resulting effects. Therefore, since changes in production are easier to implement in Ecosim than biomass changes, simulations were done perturbing production. In each simulation, the initial (Ecopath) production was kept constant for the first 10 years and then perturbed. From year 10 to year 20 of each simulation, indeed, the initial production of the functional group being observed (corresponding to the group in the row of the $\mathbf{M}$ matrix) was decreased linearly to 90% of its initial value, then maintained constant until the end of the simulation and the resulting ecosystem changes observed. Following Christensen and Walters (2004), a forcing function was used, in Ecosim, to represent this production decrease. The perturbation on the observed group produced dynamic changes on the biomass of other groups in the web. The resulting relative changes in the biomass (excluding detritus and the observed group), were compared with the corresponding elements of the row of the matrix $\mathbf{M}$. Therefore, each m_{ij} was

Table 1 – The mixed trophic impact matrix calculated by EwE for the Newfoundland model (Bundy, 2001)															
FG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	−0.035	−0.011	0.001	−0.001	0.004	−0.011	0.008	0.000	0.007	0.006	0.002	−0.002	0.019	−0.293	−0.009	−0.002
2	0.006	−0.138	−0.133	0.023	−0.017	−0.217	−0.272	−0.285	−0.015	−0.305	−0.051	−0.003	0.067	0.022	−0.104	0.076
3	0.015	0.010	−0.145	0.039	−0.022	0.055	−0.203	−0.189	0.028	0.025	−0.511	0.033	0.012	0.015	−0.019	0.031
4	−0.010	−0.007	−0.001	−0.007	−0.006	−0.008	−0.003	−0.009	−0.002	−0.001	0.003	0.001	0.004	0.008	−0.006	−0.015
5	−0.048	−0.312	−0.205	−0.389	−0.323	−0.051	−0.043	0.097	−0.310	−0.161	0.160	−0.334	−0.054	−0.196	−0.039	−0.108
6	−0.014	0.011	−0.010	−0.011	−0.009	−0.062	0.047	−0.035	−0.002	−0.019	0.004	0.023	−0.013	0.007	−0.064	−0.031
7	0.006	−0.003	0.000	0.000	−0.005	−0.092	−0.090	−0.097	−0.005	0.002	−0.007	−0.069	−0.274	−0.005	−0.041	0.006
8	−0.058	0.042	0.267	−0.028	−0.046	−0.096	−0.006	−0.195	0.012	−0.028	−0.159	0.023	0.000	0.052	−0.026	−0.093
9	−0.013	−0.030	−0.028	−0.041	−0.035	0.015	−0.001	−0.019	−0.052	−0.002	0.039	−0.043	0.010	−0.021	0.005	−0.022
10	−0.025	0.000	−0.014	−0.025	−0.017	−0.010	−0.015	−0.036	−0.026	−0.086	−0.009	−0.020	0.011	0.001	−0.030	−0.041
11	0.003	−0.001	0.121	−0.002	−0.011	0.006	−0.032	−0.023	−0.003	−0.004	−0.121	−0.010	0.003	−0.011	−0.047	0.006
12	−0.003	−0.004	−0.002	0.001	−0.005	−0.045	−0.015	0.008	0.010	0.010	0.003	−0.053	−0.057	0.013	−0.033	0.004
13	−0.002	−0.057	−0.060	−0.064	−0.033	−0.013	0.206	0.014	−0.048	0.035	0.045	0.009	−0.209	−0.035	0.018	0.005
14	0.008	−0.009	−0.008	−0.008	−0.011	−0.003	−0.011	0.008	−0.022	−0.008	0.008	−0.054	−0.047	−0.029	−0.002	0.001
15	0.005	0.021	0.061	0.012	0.015	−0.036	0.037	−0.024	−0.022	−0.053	−0.160	0.035	−0.018	−0.067	−0.195	0.005
16	0.361	−0.014	−0.025	0.214	0.251	0.107	0.184	0.514	0.052	0.170	0.010	−0.175	−0.201	−0.284	−0.075	−0.323
17	0.044	0.061	−0.023	0.027	0.020	−0.005	−0.033	−0.029	0.053	0.003	0.011	0.090	−0.020	−0.022	−0.014	−0.004
18	−0.022	0.176	−0.007	0.040	0.001	−0.038	−0.049	−0.044	−0.008	−0.071	−0.022	−0.001	−0.014	0.004	−0.017	−0.015
19	−0.002	−0.002	−0.003	0.000	0.001	0.003	0.003	0.004	−0.001	0.002	0.002	−0.004	−0.003	−0.001	−0.003	0.004
20	0.034	0.034	0.005	−0.030	−0.049	−0.070	−0.048	−0.090	−0.016	−0.036	−0.006	0.074	0.014	0.012	0.014	−0.110
21	0.009	0.004	0.098	−0.003	−0.027	−0.014	0.019	−0.011	−0.024	−0.005	−0.084	0.002	0.170	−0.012	−0.024	−0.005
22	−0.007	0.014	−0.014	−0.019	0.021	0.054	0.009	0.008	−0.018	−0.009	−0.005	0.003	0.014	0.065	−0.007	−0.009
23	0.000	−0.014	−0.025	−0.014	0.018	0.014	0.001	0.015	−0.064	−0.037	−0.073	0.203	−0.007	−0.064	−0.044	0.000
24	−0.004	−0.012	−0.040	−0.007	−0.013	−0.046	−0.004	0.004	0.174	0.026	−0.176	−0.033	−0.010	0.069	−0.091	−0.005
25	0.000	−0.005	−0.002	−0.003	0.007	−0.008	0.000	0.001	0.004	−0.021	−0.016	0.016	−0.007	0.037	0.038	0.000
26	−0.001	−0.002	0.049	−0.004	−0.001	−0.009	−0.012	−0.012	−0.041	0.061	0.319	0.101	−0.010	−0.019	0.053	0.000
27	−0.003	0.004	0.058	−0.011	0.002	0.112	0.007	−0.023	0.039	0.100	0.218	0.026	−0.008	0.124	0.289	−0.009
28	0.091	0.053	−0.011	0.075	0.025	0.101	0.071	0.045	−0.032	−0.008	−0.019	−0.024	0.264	0.070	−0.025	0.050
29	0.188	0.049	−0.001	0.081	0.077	0.031	0.065	0.136	0.018	0.038	−0.018	−0.018	0.064	−0.095	−0.016	0.198
30	0.221	0.070	−0.006	0.107	0.088	0.073	0.092	0.153	0.004	0.034	−0.026	−0.027	0.162	−0.064	−0.026	0.216
31	−0.002	−0.004	0.055	−0.029	0.009	0.090	0.003	−0.020	0.157	0.157	0.333	0.129	−0.002	0.245	0.278	−0.013
32	0.036	−0.543	−0.508	−0.658	−0.479	0.288	0.086	0.447	−0.613	0.318	0.267	−0.510	−0.042	−0.517	0.215	0.013

Table 1 (Continued)

FG	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	−0.046	0.007	−0.071	−0.290	0.013	0.027	0.016	0.010	0.009	−0.006	0.008	0.001	0.000	0.000	−0.006	−0.006
2	−0.182	−0.462	−0.425	−0.231	−0.049	−0.039	0.052	0.002	0.002	0.018	0.067	0.020	−0.009	0.005	−0.009	−0.013
3	−0.018	0.011	0.021	−0.001	−0.041	0.010	0.009	−0.011	0.007	0.045	0.031	−0.007	0.002	−0.001	−0.006	−0.020
4	−0.007	−0.016	−0.073	−0.020	−0.007	−0.007	0.001	0.003	0.000	0.000	0.003	0.006	−0.001	0.000	0.000	−0.005
5	0.078	0.140	0.088	0.054	0.060	−0.061	−0.087	0.073	0.015	0.012	−0.002	0.014	−0.001	−0.001	−0.045	0.329
6	−0.019	−0.038	−0.021	−0.032	−0.002	−0.112	−0.046	0.019	0.020	0.019	−0.026	0.010	−0.001	0.000	−0.016	−0.010
7	0.004	0.006	−0.098	0.018	0.144	0.033	0.023	−0.005	0.004	0.001	0.006	−0.006	0.001	0.000	0.002	0.007
8	0.045	−0.102	−0.048	−0.122	−0.043	−0.031	0.020	−0.010	−0.001	0.014	0.025	0.035	−0.010	0.004	0.000	−0.041
9	−0.039	0.027	0.010	0.004	0.005	0.024	−0.059	−0.057	0.017	0.036	0.003	0.007	−0.002	0.000	0.020	0.027
10	−0.031	0.006	−0.002	−0.016	0.005	−0.010	−0.039	−0.032	0.034	−0.019	−0.027	0.014	−0.004	0.001	0.018	−0.005
11	−0.003	0.006	0.001	0.003	−0.007	0.004	−0.009	0.014	0.004	−0.069	−0.025	−0.001	0.000	0.000	0.009	0.006
12	−0.024	0.004	−0.002	−0.034	0.032	0.004	−0.133	0.042	0.040	0.033	−0.001	−0.003	0.001	−0.001	−0.035	0.001
13	0.017	0.039	−0.085	0.011	−0.405	−0.041	0.009	0.000	−0.005	−0.012	0.032	0.005	−0.001	0.000	0.002	0.060
14	0.002	0.006	0.003	0.003	−0.002	−0.070	−0.037	−0.037	−0.025	0.019	−0.017	−0.001	0.001	0.000	0.020	0.008
15	−0.015	−0.039	0.000	−0.024	−0.011	−0.028	−0.115	0.012	−0.129	−0.067	−0.262	0.004	−0.002	0.001	0.035	0.001
16	−0.344	−0.158	0.017	0.330	−0.046	−0.058	−0.038	0.022	0.036	0.019	0.023	−0.170	0.044	−0.012	−0.012	0.218
17	−0.033	−0.059	−0.039	−0.045	−0.006	−0.006	−0.020	0.005	0.009	0.008	0.005	−0.038	0.004	0.002	−0.004	0.010
18	−0.029	−0.137	−0.116	−0.073	−0.013	−0.009	0.010	0.003	0.001	0.006	0.014	−0.049	0.021	−0.011	−0.001	−0.008
19	−0.002	0.000	−0.010	−0.035	−0.004	0.000	0.001	0.000	0.000	0.000	0.001	−0.001	0.000	0.000	0.000	0.002
20	0.042	0.011	0.223	−0.108	−0.088	0.010	0.008	−0.002	−0.005	−0.004	0.008	0.029	−0.007	0.001	0.000	−0.029
21	0.001	−0.024	0.142	0.015	−0.119	−0.045	0.009	0.003	0.008	0.012	−0.068	−0.050	0.018	−0.008	0.000	0.018
22	−0.004	−0.018	−0.008	−0.009	−0.011	−0.019	−0.002	0.001	0.000	−0.025	−0.024	−0.007	0.000	0.000	0.001	0.016
23	0.003	0.012	0.007	−0.002	0.014	0.005	−0.235	−0.228	−0.191	−0.185	0.077	0.011	−0.006	0.003	0.187	0.016
24	−0.002	0.006	−0.009	0.004	−0.009	−0.145	0.035	−0.312	−0.274	−0.255	−0.236	−0.016	0.009	−0.006	−0.276	−0.001
25	0.001	0.000	−0.001	−0.001	−0.002	−0.038	0.038	−0.077	−0.082	−0.074	−0.070	−0.003	0.002	−0.001	−0.049	0.004
26	−0.004	−0.001	−0.001	−0.006	−0.004	−0.050	0.119	−0.153	−0.161	−0.186	−0.141	−0.005	0.003	−0.002	−0.077	0.003
27	−0.016	−0.016	0.023	−0.016	0.039	−0.035	0.004	−0.045	−0.085	−0.082	−0.140	0.003	−0.001	0.000	0.020	0.009
28	−0.030	0.274	0.177	0.091	0.045	−0.054	−0.013	−0.014	−0.014	−0.009	−0.020	−0.320	−0.350	0.197	−0.023	0.052
29	0.229	0.102	0.015	0.067	0.149	0.050	−0.013	0.007	0.010	0.005	−0.012	−0.023	−0.469	−0.449	−0.005	0.081
30	0.217	0.202	0.080	0.100	0.164	0.114	−0.018	0.002	0.005	0.000	−0.021	0.228	0.401	−0.376	−0.014	0.102
31	−0.027	0.008	0.027	−0.014	0.025	0.241	0.270	0.389	0.378	0.370	0.408	0.044	−0.022	0.012	0.000	0.030
32	0.196	0.301	0.130	0.197	0.044	0.096	0.187	−0.003	−0.057	−0.134	−0.096	−0.032	0.009	−0.003	0.044	−0.299

Each value represents the impact of the functional group in the row (impacting group) to each functional group of the column (impacted group). Positive (or negative) values indicate that an increase of the biomass of the impacting group produce an increase (or a decrease) of the biomass of the impacted one. Functional Groups (FG): 1, whales; 2, harp seals; 3, hooded seals; 4, seabirds; 5, cod > 35 cm; 6, cod ≤ 35 cm; 7, G. halibut > 40 cm; 8, G. halibut ≤ 40 cm; 9, Aplaice > 35 cm; 10, Aplaice ≤ 35 cm; 11, flounders; 12, skates; 13, redfish; 14, L.Dem.Feeders; 15, S.Dem.Feeders; 16, capelin; 17, sand lance; 18, Arctic cod; 19, L.Pel.Feeders; 20, Pisc. SPF; 21, Plankt. SPF; 22, shrimp; 23, large crustacea; 24, echinoderms; 25, molluscs; 26, polychaetes; 27, O.Benthic Inver; 28, L.Zooplankton; 29, S.Zooplankton; 30, phytoplankton; 31, detritus; 32, fisheries.
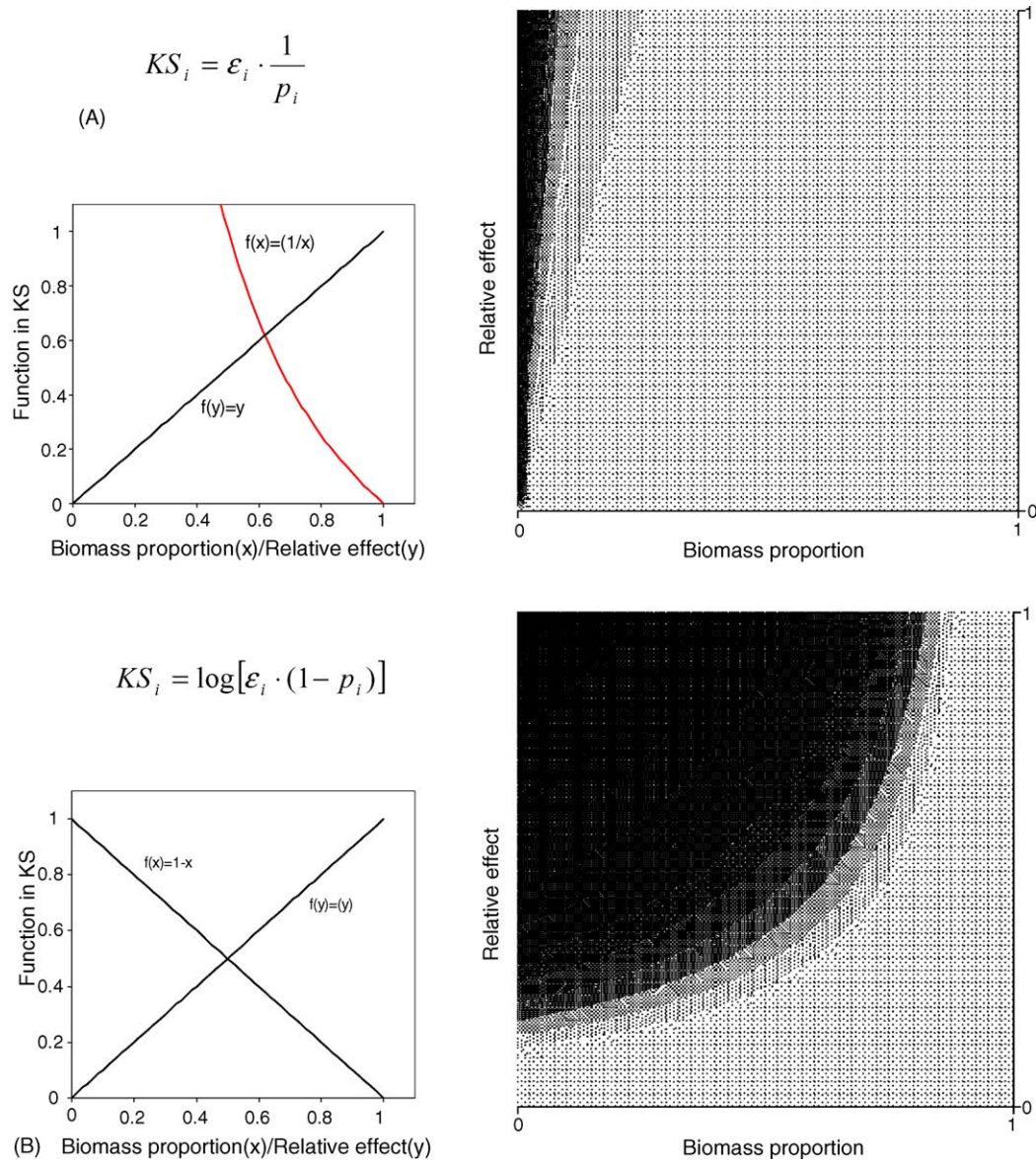
$$KS_i = \varepsilon_i \cdot \frac{1}{p_i}$$

(A)

$$KS_i = \log\left[\varepsilon_i \cdot (1 - p_i)\right]$$

(B) Biomass proportion(x)/Relative effect(y)

Fig. 1 – Graphic comparison of the keystoneness index calculated as: (A) suggested by Power et al. (1996), and (B) proposed in this work. On the left are represented the functions of biomass proportion and of overall effect in the index. On the right the values of the index (dark, high values of KS index; light, low values) on the basis of biomass proportion and relative overall effect as entries.

compared with:

$$S_{i,j} = \left(\frac{B_j^e - B_j^s}{B_j^s} \right)_{\delta P_i}$$

(3)

where B_j^e and B_j^s is the biomass of the impacted group at the end and at the start, respectively, of the simulation with perturbed production of the impacting group (δP_i).

Three models were used to test the correspondence between the S_{ij} obtained with Ecosim and the m_{ij} estimated by Ecopath: a model of the Prince William Sound ecosystem, comprised of 48 functional groups (Okey and Pauly, 1999); a model for the Gulf of Thailand, with 40 functional groups (Christensen, 1998), and a model of the North Pacific, with 31 functional groups (Cox et al., 2002), all selected because they are highly detailed and well documented.

Fig. 2 – Prince William Sound model: comparison between the relative changes in biomass obtained by the dynamic simulations and the mixed trophic impacts. For each simulation, corresponding to a plot, the production of the impacting group (target) was lowered by 10%. The relative changes in the biomasses of the other groups are compared with the corresponding mixed trophic impact values, in terms of ranking order, and the Spearman's correlation coefficient is reported to assess the agreement.
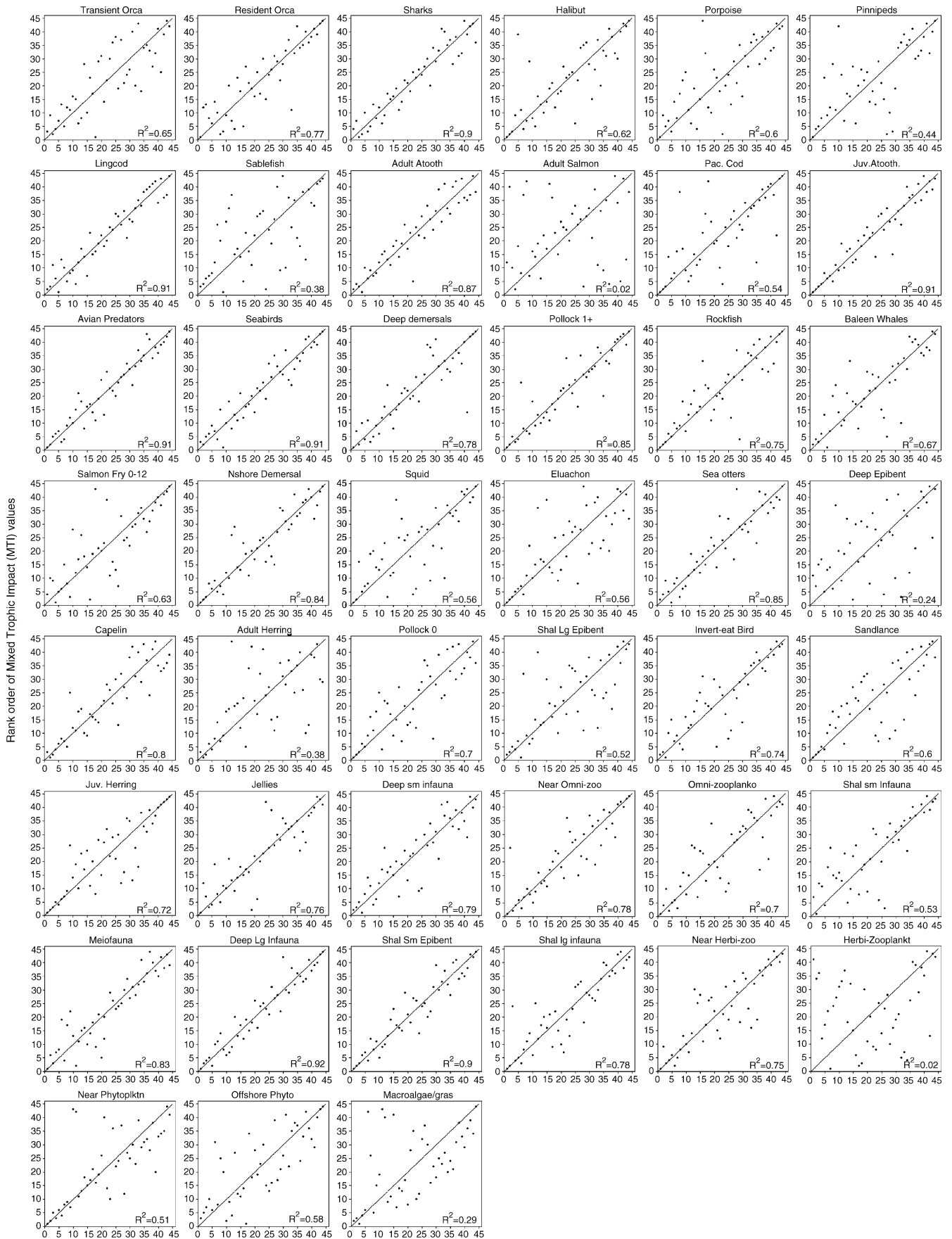
Rank order of relative changes of biomass estimated by means of Ecosim simulations

Fig. 2

2.5. Estimating total impact

Given that there is agreement between the m_{ij} and S_{ij} (see below), it is appropriate to estimate the total impact of one functional group on the ecosystem through the mixed trophic impact. Since each impact can be either negative or positive, we define our proposed measure of the overall effect of each group as

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2} \qquad (4)$$

in which the effect of the change in biomass on the group itself (i.e., m_{ii}) is not included.

The normalized flows in Eq. (2) bound the sum of the elements of the rows and columns of matrix **Q** between the interval -1 to $+1$ (Ulanowicz and Puccia, 1990), which guarantees that the overall effect, estimated as the sum of the elements of **M** as in Eq. (4), does not need to be weighted by the numbers of groups used to describe the trophic network.

Accounting for the positive and negative contributions to the overall effect estimated as in Eq. (4), allows evidencing for a given group, respectively, bottom-up and top-down effects contributing to its overall effect.

2.6. Identifying an index of keystoneness

Several alternatives for combining overall effect and biomass in our keystoneness index were explored. The biomass component was adequately represented by the contribution of the functional group to the total biomass of the food web (Power et al., 1996), that is:

$$p_i = \frac{B_i}{\sum_k B_k} \qquad (5)$$

The index calculated as suggested by Power et al. (1996), that is:

$$\text{KS}_i = \varepsilon_i \frac{1}{p_i} \qquad (6)$$

was strongly influenced by the biomass proportions, attributing high keystoneness to functional groups with low biomass (as required) and low overall effect (which should not be the case; see Fig. 1A).

Therefore, in order to balance the two components (overall effect and biomass), we define our index of keystoneness as follows:

$$\text{KS}_i = \log[\varepsilon_i (1 - p_i)] \qquad (7)$$

This index has the property of attributing high values of keystoneness to functional groups that have both low biomass proportion and high overall effect (Fig. 1B), therefore identifying the keystone species in accordance with the requirements stated in the Introduction. As should be the case, this index assigns low keystoneness to groups with high effect but high biomass as well, e.g., structuring and dominant functional

groups such as macrophytes. Moreover, the negative and positive contributions to the overall effect, as outlined above, allow calculating the bottom-up and top-down effects contributing to the keystoneness index of Eq. (7).

The estimation of the total impacts and of the 'keystoneness' proposed here (Eq. (7)) was applied to each living functional group (thus excluding detritus groups) of a suite of 33 Ecopath models considered well described and detailed, i.e., with a minimum of 24 functional groups used for describing the ecosystem. These models represent the trophic web of marine ecosystems that differ for location, period and type of habitat represented. The proposed analysis was applied also to 9 models representing different upwelling ecosystems in different periods, for a total of 42 models analysed.

3. Results

The comparison between the observed changes resulting from the Ecosim simulations, S_{ij}, and the changes predicted by means the mixed trophic impact, m_{ij}, are given in Figs. 2–4, respectively, for the Prince William Sound, the Gulf of Thailand and the North Pacific model. The comparisons showed, with few exceptions, a high Spearman's (rank) correlation (Zar, 1999) between changes observed by means of the dynamic simulation (abscissa) and the correspondent row of the matrix **M** (ordinate of each plot of the figures). The bisecting line is also shown, together with the rank correlation coefficient between observed and predicted values. The Prince William Sound functional groups (Fig. 2), showed low rank correlations only for the herbivorous zooplankton and adult salmon (both with $R^2 = 0.02$), while the analysis on the Gulf of Thailand model (Fig. 3) resulted in low correlations for rays ($R^2 = 0.03$), phytoplankton ($R^2 = 0.05$), 'trashfish' ($R^2 = 0.09$), *Priacanthus* spp. ($R^2 = 0.12$) and juveniles *Nemipterus* spp. ($R^2 = 0.13$). The lowest rank correlation for the North Pacific model (Fig. 4) was $R^2 = 0.17$ for the large blue shark group. However, most of the functional groups show high agreement between simulated biomass change and mixed trophic impacts. Thus the overall rank correlations were 54.8%, 51.5% and 54.5%, respectively, for the Prince William Sound, the Gulf of Thailand and the North Pacific. Results of non-parametric test of correlation significance (Zar, 1999) evidenced that the above reported overall rank correlations are all significant at $p < 0.001$.

The high agreement between the m_{ij} and S_{ij}, show that it is legitimate to use Eq. (4) to draw inferences on total impacts from the **M** matrix, and subsequently applying Eq. (7) to calculate the 'keystoneness' of its various functional groups. Fig. 5 represents the estimated keystoneness index for the functional groups of four selected models, representing the ecosystems of Newfoundland (after Bundy, 2001), Eastern Tropical Pacific (Watters et al., 2003), Chesapeake Bay (Baird and Ulanowicz, 1989) and Bolinao reef (Aliño et al., 1993).

As might be seen, the keystoneness index estimated here show a common pattern in different ecosystems, and allows ranking the groups of each model by decreasing keystoneness. The keystone functional groups are those that have value of the proposed index close to or greater than zero.
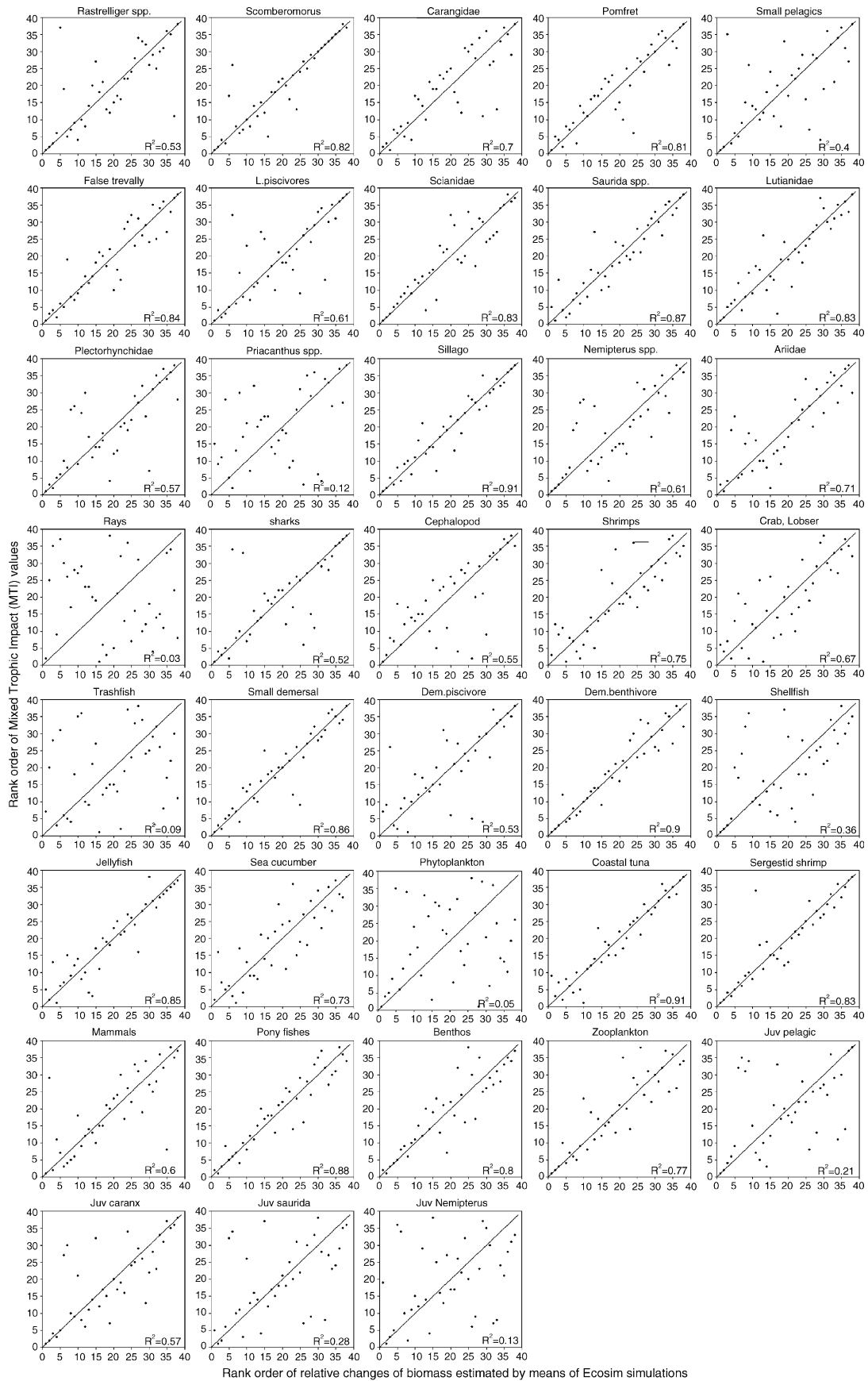
Fig. 3 – Gulf of Thailand model: comparison between the changes in biomass obtained by the dynamic simulations and the mixed trophic impacts.
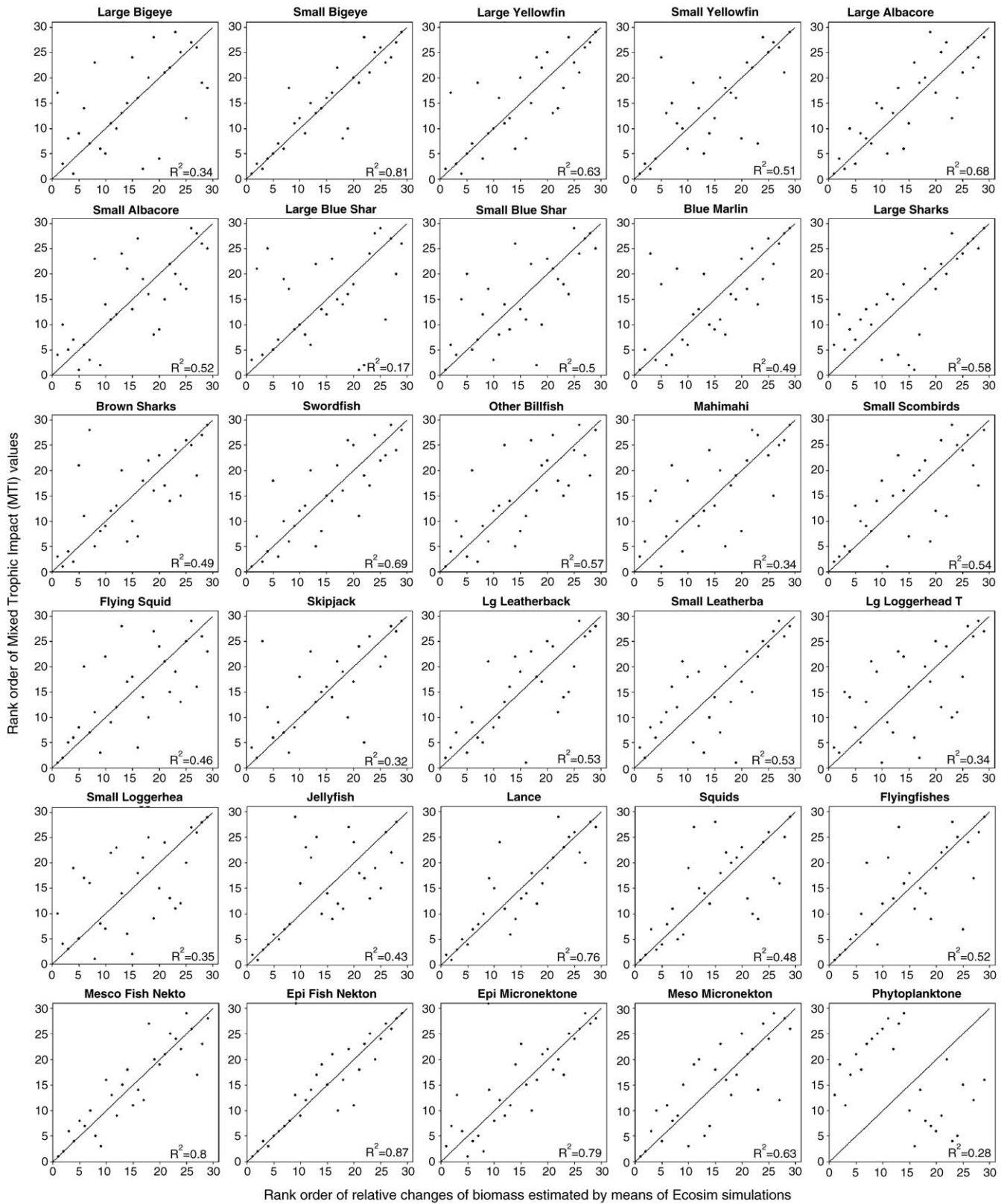
Fig. 4 – North Pacific model: comparison between the changes in biomass obtained by the dynamic simulations and the mixed trophic impacts.
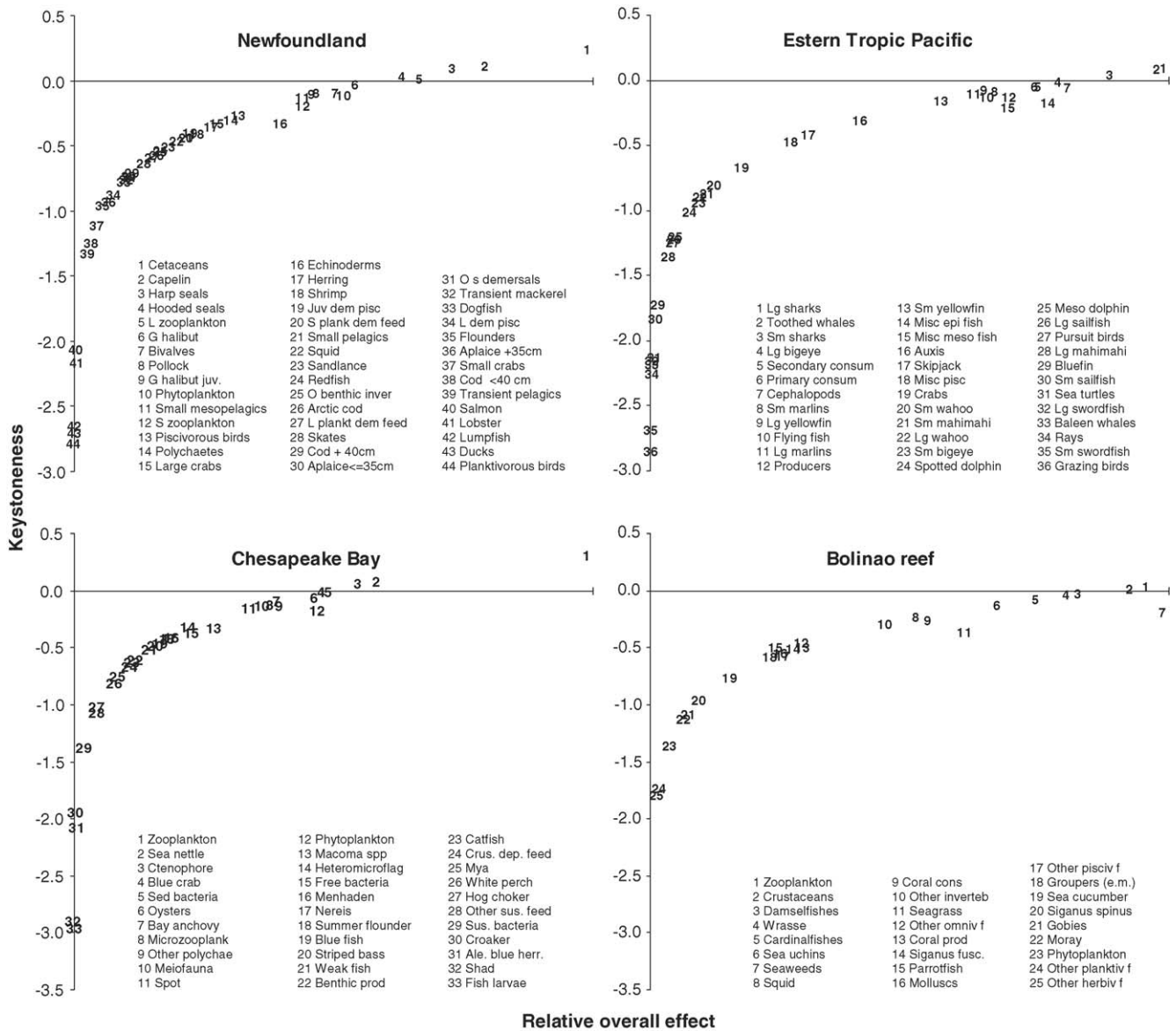
Fig. 5 – Keystoneness for the functional groups of four marine trophic webs. For each functional group, the keystoneness index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web, thus for x axis the scale is always between 0 and 1. Within each trophic web the species are ordered by decreasing keystoneness, therefore the keystone functional groups are those ranking between the first groups.

Different groups of marine mammals (cetaceans, harp and hooded seals) show high keystoneness in the Newfoundland ecosystem, where capelin, a forage species, ranks second. Toothed whales rank second in the Eastern Pacific, between large and small sharks, which rank first and third, respectively. For the Chesapeake and Bolinao ecosystems, zooplankton has the highest keystoneness.

Tables 2 and 3 lists, for the 42 Ecopath models analysed, the four functional groups that ranked highest in term of their keystoneness. The top-down effect as percentage contributions to the keystoneness for each species, evaluated through the proportion of the negative values contributing to the sum in Eq. (4), is also reported in Tables 2 and 3.

Table 2 contains the results of the analysis applied to 33 models considered well described and detailed on the basis of the number of groups used to describe the ecosystems (minimum 24 groups, maximum 59 groups). Marine mammals often have high keystoneness, and rank first (Alaska gyre, Azores, Newfoundland, Norwegian Barents Sea models) or second (Easter tropic Pacific models, Floreana, Georgia Strait, Newfoundland 1985–1987) in many models. Sea birds rank third in Lancaster model and fourth in the Prince William Sound model. Sharks and rays have high keystoneness in many ecosystems, ranking first (Biscaya, Easter tropic Pacific, Floreana, Hong Kong, Morocco models) or second (Gulf of Thailand and Western Gulf of Mexico) in many models. All these

Table 2 – The first four functional groups ranking in decreasing order of keystoneness resulting from the analysis of 33 detailed Ecopath models

Model	Keystoneness rank order			
	1	2	3	4
Alaska gyre (Pauly et al., 1996)	Orca-transient (TL 3.89) KS = 0.074 (td = 84%)	Squids (TL 1.84) KS = 0.034 (td = 28%)	Small pelagics (TL 2.51) KS = −0.037 (td = 72%)	Phytoplankton (TL 1) KS = −0.12 (td = 21%)
Azores 1997 (Guénette and Morato, 2001)	Killer whales (TL 5.34) KS = 0.107 (td = 69%)	Cephalop L (TL 4.5) KS = 0.053 (td = 90%)	Dolphins (TL 4.77) KS = −0.006 (td = 63%)	Coastal L pred (TL 4.17) KS = −0.05 (td = 100%)
Biscaya 1970 (Ainsworth et al., 2002)	Large sharks (TL 4.02) KS = 0.254 (td = 85%)	Primary producers (TL 1) KS = −0.017 (td = 2%)	Toothed cetaceans (TL 4.14) KS = −0.071 (td = 99%)	Zooplankton small (TL 2) KS = −0.15 (td = 25%)
Biscaya 1998 (Ainsworth et al., 2002)	Large sharks (TL 4.04) KS = 0.291 (td = 83%)	Primary producers (TL 1) KS = −0.021 (td = 2%)	Toothed cetaceans (TL 4.15) KS = −0.021 (td = 97%)	Zooplankton small (TL 2) KS = −0.15 (td = 25%)
Bolinao reef (Aliñó et al., 1993)	Zooplankton (TL 2.06) KS = 0.026 (td = 75%)	Crustaceans (TL 2.59) KS = 0.01 (td = 29%)	Damselfishes (TL 2.48) KS = −0.038 (td = 69%)	Wrasse (c.a.) (TL 3.57) KS = −0.05 (td = 99%)
Cantabrian Sea 1994 (Sánchez and Olaso, 2004)	Small Dem Fish (TL 3.66) KS = −0.112 (td = 90%)	Zoopl suprabenthic (TL 2.8) KS = −0.163 (td = 71%)	Blue whiting (TL 3.84) KS = −0.19 (td = 54%)	Phytoplankton (TL 1) KS = −0.238 (td = 5%)
Chesapeake Bay (Baird and Ulanowicz, 1989)	Zooplankton (TL 2.17) KS = 0.299 (td = 13%)	Sea nettle (TL 3.45) KS = 0.073 (td = 52%)	Ctenophore (TL 3.03) KS = 0.043 (td = 92%)	Blue crab (TL 3.74) KS = −0.027 (td = 98%)
Central North Pacific (Cox et al., 2002)	Squids (TL 3.1) KS = −0.051 (td = 87%)	Jellyfish (TL 3)) KS = −0.061 (td = 0%)	Epi Fish Nekton (TL 3) KS = −0.177 (td = 37%)	Phytoplankton (TL 1) KS = −0.184 (td = 0%)
Eastern Bering Sea 1950 (Trites et al., 1999)	Large zoops (TL 2.27) KS = −0.067 (td = 36%)	Benth.P.Feeders (TL 2.82) KS = −0.078 (td = 75%)	Pelagics (TL 3.25) KS = −0.086 (td = 13%)	Phytoplankton (TL 1) KS = −0.152 (td = 3%)
Eastern tropical Pacific (Watters et al., 2003)	Lg. sharks (TL 5.08) KS = 0.088 (td = 99%)	Toothed whales (TL 5.39) KS = 0.085 (td = 98%)	Sm sharks (TL 5.4) KS = 0.035 (td = 99%)	Lg. bigeye (TL 5.34) KS = −0.018 (td = 66%)
Floreana, Galapagos (Okey et al., 2004a)	Sharks (TL 4.13) KS = 0.373 (td = 62%)	Sea lions (TL 4.01) KS = 0.335 (td = 82%)	Pel predators (TL 3.86) KS = 0.216 (td = 49%)	Benthic algae (TL 1) KS = 0.159 (td = 4%)
Georgia Strait 1950 (Pauly et al., 1998; Walters et al., 2005)	C. Zoolplankton (TL 2.4) KS = 0.015 (td = 26%)	Transient orcas (TL 5.48) KS = −0.051 (td = 66%)	Seals Sealions (TL 4.51) KS = −0.054 (td = 58%)	Lingcod (TL 4.17) KS = −0.064 (td = 95%)
Gulf of Maine (Heymans, 2001)	Large pelagic feeders (TL 4.54) KS = 0.069 (td = 93%)	Macrozooplankton (TL 2.72) KS = −0.087 (td = 25%)	Small demersal feeders (TL 3.36) KS = −0.089 (td = 76%)	Large demersal feeders (TL 3.96) KS = −0.14 (td = 97%)
Gulf of St. Lawrence 1986 (Morissette et al., 2003)	Large cod (TL 3.86) KS = 0.053 (td = 84%)	Large zooplankton (TL 2.44) KS = −0.016 (td = 24%)	Capelin (TL 3.27) KS = −0.028 (td = 70%)	Cetacea (TL 4.08) KS = −0.039 (td = 93%)

Model	Keystoneness rank order			
	1	2	3	4
Gulf of Thailand 1973 (Christensen, 1998; FAO/FISHCODE, 2001; Walters et al., 2005)	Zooplankton (TL 2) KS = −0.024 (td = 23%)	Rays (TL 3.13) KS = −0.033 (td = 100%)	Mammals (TL 3.69) KS = −0.036 (td = 84%)	Trashfish (TL 2.56) KS = −0.07 (td = 68%)
Hong Kong Preliminary (Cheung et al., 2002; Buchary et al., 2002)	Large sharks Ad. (TL 4.28) KS = −0.013 (td = 72%)	Zooplanktons (TL 2) KS = −0.087 (td = 31%)	Sm. pelagics (TL 2.94) KS = −0.156 (td = 79%)	Macrozoobenthos (TL 2.38) KS = −0.184 (td = 69%)
Lancaster (Mohammed, 2001)	Arctic cod (TL 3.32) KS = 0.238 (td = 23%)	Mertensia ovum (TL 2.98) KS = 0.075 (td = 96%)	Glaucous gulls (TL 4.53) KS = −0.103 (td = 91%)	Narwhal (TL 4.53) KS = −0.149 (td = 77%)
Morocco 1984 (Stanford et al., 2001)	Lg. demersal sharks/rays (TL 4.2) KS = 0.153 (td = 98%)	Med. pelagic comm. (TL 3.51) KS = 0.132 (td = 51%)	Pelagic sharks (TL 4.37) KS = 0.112 (td = 95%)	Cephalopods (TL 3.49) KS = 0.029 (td = 79%)
Newfoundland 1995–2000 (Bundy, 2001)	Cetaceans (TL 4.02) KS = 0.227 (td = 98%)	Capelin (TL 3.27) KS = 0.101 (td = 42%)	Harp seals (TL 4.14) KS = 0.089 (td = 84%)	Hooded seals (TL 4.85) KS = 0.027 (td = 77%)
Newfoundland 1900 (Heymans, 2003)	Cetaceans (TL 4.02) KS = 0.261 (td = 94%)	Capelin (TL 3.27) KS = 0.148 (td = 41%)	Hooded seals (TL 4.72) KS = 0.105 (td = 76%)	Cod + 40 cm (TL 4.07) KS = 0.102 (td = 91%)
Newfoundland 1985–1987 (Bundy, 2001; Heymans et al., 2004)	Capelin (TL 3.27) KS = −0.025 (td = 33%)	Harp seals (TL 4.4) KS = −0.041 (td = 98%)	Cod > 35 cm (TL 4.17) KS = −0.089 (td = 88%)	Phytoplankton (TL 1) KS = −0.186 (td = 1%)
North Sea 1880 (Mackinson, 2001)	Other predatory fish (TL 4.34) KS = 0.152 (td = 94%)	Bluefin tuna (TL 4.58) KS = −0.039 (td = 100%)	Zooplankton (TL 2.12) KS = −0.084 (td = 12%)	Other crustaceans (TL 2.59) KS = −0.09 (td = 5%)
North Sea 1963–1999 (FC database)	Euphausiids (TL 3.22) KS = 0.065 (td = 54%)	Sandeel (TL 3.67) KS = −0.052 (td = 29%)	O.invertebrates (TL 2.57) KS = −0.072 (td = 78%)	Copepods (TL 2.11) KS = −0.164 (td = 45%)
North Sea 1974–1995 (FC database)	Euphausiids (TL 3.22) KS = 0.064 (td = 54%)	Sandeel (TL 3.67) KS = −0.053 (td = 29%)	O.invertebrates (TL 2.57) KS = −0.072 (td = 78%)	Copepods (TL 2.11) KS = −0.164 (td = 45%)
North Coast-Central Java (Buchary, 1999)	Phytoplankton (TL 1) KS = −0.019 (td = 5%)	Macrozoobenthos (TL 2.29) KS = −0.027 (td = 69%)	Sm. herb. zoop. (TL 2) KS = −0.036 (td = 52%)	Lg. dem pred (A) (TL 3.87) KS = −0.056 (td = 91%)
Norwegian Barents Sea 1950 (Dommasnes et al., 2001)	Seals (TL 3.93) KS = −0.022 (td = 77%)	Phytoplankton (TL 1) KS = −0.09 (td = 1%)	Toothed whales (TL 4.21) KS = −0.107 (td = 91%)	Small zooplankt (TL 2) KS = −0.119 (td = 29%)
Norwegian-Barents Sea 1997 (Dommasnes et al., 2001)	Seals (TL 4.05) KS = −0.081 (td = 92%)	Phytoplankton (TL 1) KS = −0.097 (td = 2%)	Cod 4+ (TL 4.26) KS = −0.134 (td = 87%)	Other benthic fish (TL 3.58) KS = −0.136 (td = 77%)

Table 2 (Continued)

Table 2 (*Continued*)

Model	Keystoneness rank order			
	1	2	3	4
Prince William Sound (Okey and Pauly, 1998; Okey and Pauly, 1999)	Offshore Phyto. (TL 1) KS = 0.027 (td = 11%)	Near phytoplankton (TL 1) KS = 0.023 (td = 4%)	Omni-zooplankton (TL 2.25) KS = 0.009 (td = 12%)	Avian predators (TL 3.92) KS = −0.014 (td = 85%)
Scotian shelf 1980–1985 (Bundy and Guénette, 2002)	Dem. Piscivores (TL 4.45) KS = −0.014 (td = 100%)	Cod > 40 cm (TL 3.77) KS = −0.045 (td = 86%)	LZP (TL 2.56) KS = −0.083 (td = 25%)	Cetaceans (TL 3.78) KS = −0.116 (td = 93%)
South19 Atlantic States (Okey and Pugliese, 2001)	Squid (TL 3.08) KS = 0.069 (td = 80%)	Benthic macrofauna (and meiofauna) (TL 2.04) KS = 0.012 (td = 76%)	Groupers (TL 3.99) KS = −0.002 (td = 99%)	Zooplankton (TL 2) KS = −0.046 (td = 25%)
US Mid Atlantic Bight (Christensen, 1998)	Goosefish (TL 4.36) KS = 0.076 (td = 99%)	Forage fish (TL 3.36) KS = 0.07 (td = 45%)	Small crustaceans (TL 2.11) KS = −0.099 (td = 56%)	Dolphins and porpoise (TL 4.41) KS = −0.112 (td = 95%)
West Florida Shelf (Okey et al., 2004b)	Small mobile epifauna (TL 2.35) KS = 0.042 (td = 86%)	PelCoasPisc (TL 4.27) KS = 0.02 (td = 93%)	Microbial heterotrophs (TL 2) KS = −0.055 (td = 88%)	Squid (TL 3.78) KS = −0.056 (td = 74%)
Western Gulf of Mexico (Arreguín-Sánchez et al., 1993, 2004)	Jacks (TL 3.77) KS = 0.112 (td = 98%)	Sharks (TL 4.78) KS = 0.066 (td = 74%)	Red grouper (TL 4.29) KS = 0.011 (td = 32%)	Red snapper (TL 4.01) KS = −0.06 (td = 68%)

For each functional group, along with its keystoneness (KS), is reported the fraction of the total impact produced by top-down effects (td). The trophic level (TL) of each group is also reported as estimated by Ecopath with Ecosim.

Table 3 – The first four groups ranking in decreasing order of keystoneness resulting from the analysis of the nine Ecopath models of upwelling ecosystems				
Model	Keystoneness rank order			
	1	2	3	4
California 1965–1972 (Jarre-Teichmann and Christensen, 1998)	Marine birds (TL 3.73) KS = 0.139 (td = 97%)	Marine mammals (TL 3.92) KS = −0.113 (td = 98%)	Phytoplankton (TL 1) KS = −0.246 (td = 3%)	Zooplankton (TL 2.11) KS = −0.248 (td = 40%)
California 1977–1985 (Jarre-Teichmann and Christensen, 1998)	Marine birds (TL 3.73) KS = −0.109 (td = 93%)	Mackerel (TL 3.27) KS = −0.152 (td = 87%)	Marine mammals (TL 3.92) KS = −0.193 (td = 100%)	Zooplankton (TL 2.11) KS = −0.219 (td = 39%)
NBenguela Namibia 1971–1977 (Jarre-Teichmann and Christensen, 1998; Heymans et al., 2004)	Zooplankton (TL 2.11) KS = −0.168 (td = 53%)	Phytoplankton (TL 1) KS = −0.175 (td = 3%)	Hake (TL 3.43) KS = −0.228 (td = 96%)	Macrobenthos (TL 2.16) KS = −0.304 (td = 91%)
NBenguela Namibia 1978–1983 (Jarre-Teichmann and Christensen, 1998)	Phytoplankton (TL 1) KS = −0.17 (td = 6%)	Zooplankton (TL 2.11) KS = −0.224 (td = 56%)	Anchovy (TL 2.44) KS = −0.24 (td = 15%)	Macrobenthos (TL 2.16) KS = −0.277 (td = 91%)
NW Africa Upwelling 1970–1979 (Jarre-Teichmann and Christensen, 1998)	Horse mackerel (TL 3.28) KS = −0.101 (td = 93%)	Other pelagics (TL 3) KS = −0.137 (td = 92%)	Phytoplankton (TL 1) KS = −0.153 (td = 4%)	Zooplankton (TL 2.11) KS = −0.221 (td = 60%)
Peru 1950 (Jarre-Teichmann, 1992)	Horse Mackerel (TL 3.27) KS = 0.084 (td = 100%)	Anchoveta (TL 2.21) KS = 0.039 (td = 7%)	Phytoplankton (TL 1) KS = −0.141 (td = 8%)	Zooplankton (TL 2.05) KS = −0.274 (td = 85%)
Peru 1960 (Jarre-Teichmann et al., 1991; Jarre-Teichmann, 1992)	Cormorant (TL 3.58) KS = −0.065 (td = 89%)	Anchoveta (TL 2.21) KS = −0.127 (td = 14%)	Phytoplankton (TL 1) KS = −0.174 (td = 10%)	Zooplankton (TL 2.05) KS = −0.277 (td = 81%)
Peru 1964–1971 (Jarre-Teichmann and Christensen, 1998)	Lg. scombrids (TL 3.49) KS = −0.135 (td = 97%)	Phytoplankton (TL 1) KS = −0.243 (td = 18%)	Zooplankton (TL 2.11) KS = −0.255 (td = 70%)	Meiobenthos (TL 2) KS = −0.266 (td = 86%)
Peru 1973–1981 (Jarre-Teichmann and Christensen, 1998)	Horse mackerel (TL 3.38) KS = −0.235 (td = 89%)	Zooplankton (TL 2.11) KS = −0.247 (td = 58%)	Anchovy (TL 2.44) KS = −0.275 (td = 52%)	Phytoplankton (TL 1) KS = −0.314 (td = 7%)

Keystoneness (KS), proportion of top-down effect (td) and trophic level (TL) are reported.

functional groups have effects on the other components of the ecosystem mainly via top-down impacts.

A few ecosystems (North Coast Central Java, Prince Williams Sound) show high keystoneness for phytoplankton, while in coastal and semi-enclosed marine environments (Bolinao reef, Chesapeake Bay, Georgia Strait, Gulf of Thailand), the zooplankton group has high keystoneness.

Table 3 presents analogous results for the nine models of upwelling ecosystems. The seabirds are important in the California (both models) and Peru (1960) upwelling ecosystems, while marine mammals rank second and third in the California models. Mackerel has high keystoneness in California (77–85), Peru and Northwest Africa. The zooplankton and phytoplankton groups rank for keystoneness among the first four in all the upwelling ecosystems analysed. Moreover, models of the same upwelling system in different periods seem to show an increase of keystoneness of intermediate trophic levels concomitant with a decrease of keytoneness of top predators over time: marine mammals are ranking second in California model for 1965–1972 while they rank third in the model for the later period (1977–1985); in Peru 1960 cormorants are ranking first while later periods show high keystoneness for lower TL functional groups (large scombrids in 1964–1971 and horse mackerel in 1973–1981).

4.   Discussion

The high general agreement between the mixed trophic impacts estimated by the mass-balance routine, Ecopath, and the observed relative changes in the biomasses obtained with long-term Ecosim simulations, allowed use of the mixed trophic impact matrix **M** as a straightforward basis to quantify the effect one functional group has on all the other groups in the ecosystem. Thus, the method proposed allows estimating the keystoneness of the species or group of species in a model without having to perform the time-dynamic simulations, as performed, e.g. by Okey et al. (2004a), thus avoiding differences induced by different simulation protocols.

The wide use of EwE and the easy implementation of the method proposed here allow standardizing the procedure to estimate the keystoneness of functional groups in models of different marine ecosystems and of the same ecosystem at different periods or scales. Although the methodology has the potential for ranking groups across models we examined here rankings of keystoneness within models.

Generally, marine mammals ranked high in most ecosystems, but in some, they had low rank; thus, spotted dolphin and baleen whales rank 24 and 33 in Eastern Pacific model. Similarly, skates and sharks ranked high in the Newfoundland model, but very low in the Eastern tropical Pacific model (dogfish was only 30th). Seabirds appear to have high keystoneness in shallow and very productive environments (upwelling systems), but low keystoneness in open seas, ranking e.g., last in Newfoundland and the Easter Tropic Pacific. In shallow coastal ecosystems, phyto- and zooplankton can have high keystoneness. Indeed, the lower part of the trophic web appears to be very important in these ecosystems, where other benthic groups also tend to have high keystoneness index.

Thus, we concur with Power et al. (1996) and Piraino et al. (2002), that keystones are not straightforwardly predicable. Certainly, and perhaps surprisingly, there is no general correlation between trophic level and keystoneness.

The index proposed assign low keystoneness to functional groups with high abundance, whether they have high impacts or not, thus allowing us to distinguish between keystone species, and dominant and structuring species—with which keystones must not be confounded (Power et al., 1996). Macrobenthic producers generally have low keystoneness, e.g., in the Bolinao reef model, where seagrasses and seaweeds have low keystoneness index.

Another important result is that keystone species do not always exert their high impact by means of top-down effects, a feature initially suggested to be a defining characteristic of keystone species (Paine, 1969), and thus proposed for identifying keystones (Davic, 2003). In fact, although results highlight that keystone functional groups exert their effect via top-down in many ecosystems (e.g., Newfoundland and Eastern tropical Pacific), keystoneness via bottom-up effects appears also very important in others (e.g., North Sea, Prince Williams Sound). These results are not contradicting previous works highlighting the high importance of top-down effects in keystoneness (Paine, 1966; Menge et al., 1994; Estes et al., 1998) and confirm that bottom-up influences can also be important (Bustamante et al., 1995; Menge, 1995). Moreover, upwelling systems show a prevalence of keystone functional groups with intermediate positions in trophic webs. This indicates that these intermediate functional groups contribute to the mixture of top-down and bottom-up control typical of wasp-waist ecosystems (Cury et al., 2000). Moreover, changes over time of keystone functional groups in upwelling systems seem to evidence the increase of keystoneness of intermediate functional groups and the concomitant decrease of keystoneness of high trophic level groups thus suggesting an increase of wasp-waist control over time.

5.   Conclusion

Since the first definition of keystone species by Paine (1969), their importance for conservation purposes has been widely recognized. However, difficulties in experimental approaches and the different roles assumed by species in time and space (Paine, 1994; Menge et al., 1994; Estes et al., 1998) lead to increasing scepticism about the original definition of the keystone species concept and the flourishing of different definitions (Mills et al., 1993; Bond, 2001; Davic, 2003). Therefore, although the importance of the concept is well recognized, a widely accepted approach for quantifying keystoneness is still lacking (Bond, 2001).

The straightforward methodology proposed here may contribute to filling this gap. The mixed trophic matrix upon which it relies allows including direct and indirect effects of trophic interactions. Moreover, the broad use of EwE will facilitate application of the methodology to the large number of ecosystems for which models exist, thus providing a broad empirical basis for the new approach. In view of the key role experiments must continue to play (Paine, 1966, 1994; Menge et al., 1994; Power et al., 1996) the methodology proposed can

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