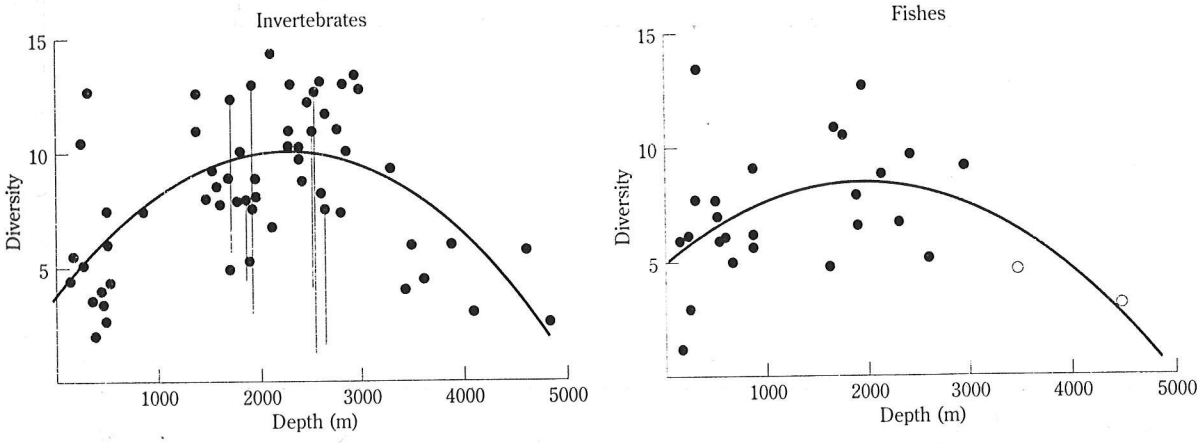
Université de Nantes **Faculté des Sciences**

PALEOENVIRONNEMENT ET BIODIVERSITE

PROF. P. G. BENINGER

QUELQUES ILLUSTRATIONS DU COURS



Université de Nantes **Faculté des Sciences**

PALEOENVIRONNEMENT ET BIODIVERSITE

Thématique Biodiversité – Prof. P. Beninger

- Situation générale du champ d'étude : la biologie théorique
- Bases de la biodiversité : concept d'espèce, taxons/clades
- Biodiversité : définition, évaluation ; indices de biodiversité, considérations théoriques et pratiques
- Echelles de mesure et biodiversité
- Diversité vs Disparité ; relations avec micro- et macro-évolution
- Relation diversité- stabilité de l'écosystème
- Facteurs écologiques producteurs de la diversité
- Facteurs écologiques réducteurs de la diversité
- Relation diversité – invasion
- Relations diversité – fonctions et services de l'écosystème
- Effets anthropiques négatifs
- Effets/options anthropiques positifs
- Sujets d'actualité scientifique en biodiversité

PROGRESS TOWARD A GENERAL SPECIES CONCEPT

Bernhard Hausdorf[1,2]

[1]*Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany*

[2]*E-mail: hausdorf@zoologie.uni-hamburg.de*

New insights in the speciation process and the nature of "species" that accumulated in the past decade demand adjustments of the species concept. The standing of some of the most broadly accepted or most innovative species concepts in the light of the growing evidence that reproductive barriers are semipermeable to gene flow, that species can differentiate despite ongoing interbreeding, that a single species can originate polyphyletically by parallel evolution, and that uniparental organisms are organised in units that resemble species of biparental organisms is discussed. As a synthesis of ideas in existing concepts and the new insights, a generalization of the genic concept is proposed that defines species as groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact. The benefits of this differential fitness species concept are that it classifies groups that keep differentiated and keep on differentiating despite interbreeding as species, that it is not restricted to specific mutations or mechanisms causing speciation, and that it can be applied to the whole spectrum of organisms from uni- to biparentals.

KEY WORDS: Hybridization, introgression, speciation.

① but requires fore knowledge of fitness effects in all other groups!

② also requires reliable information on success rate of exchange!

Table 1. Classification of groups of individuals as species (+), usually species (±) or not separate species (–) by different species concepts (na, concept not applicable). BSC=biological species concept; PSC=phylogenetic species concept; GCD=genotypic cluster definition; CSC=cohesion species concept; GSC=genic species concept; DFSC=differential fitness species concept.

	BSC	PSC	GCD	CSC	GSC	DFSC
Groups of uniparentals that are characterized by features that would have negative fitness effects in other groups	na	+	±	+	+	+
Diagnosable groups that are not characterized by features that cannot be exchanged with other groups, but do not exchange genes with other groups because of geographical isolation	–	+	–	–	–	–
Diagnosable groups of uniparentals that are not characterized by features that would have negative fitness effects in other groups	na	+	±	–	–	–
Groups of biparentals that are reproductively isolated but occupy the same niche	+	+	±	–	+	+
Groups that are differentially adapted and are not able to share the genes controlling these adaptive characters, although they are interbreeding	–	–	±	–	+	+
Groups of biparentals that are reproductively isolated due to non-genic mutations or processes other than differential adaptation	+	+	±	±	–	+

© 2011 The Author(s). *Evolution* © 2011 The Society for the Study of Evolution.

Evolution 65-4: 923–931

Problem ② : eg. hybrid sunflowers → new species for sure, but resulted from a process of very irregular exchange!

Rappel : Darwin 'On the origin of species' = 1859

THE SPECIES CONCEPT AS AN EMERGENT PROPERTY OF POPULATION BIOLOGY

Michael W. Hart[1,2]

[1]*Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada*

[2]*E-mail: mwhart@sfu.ca*

Resurgent interest in the genetics of population divergence and speciation coincides with recent critical evaluation of species concepts and proposals for species delimitation. An important result of these parallel trends is a slight but important conceptual shift in focus away from species diagnoses based on prior species concepts or definitions, and toward analyses of the processes acting on lineages of metapopulations that eventually lead to differences recognizable as species taxa. An advantage of this approach is that it identifies quantitative metapopulation differences in continuous variables, rather than discrete entities that do or do not conform to a prior species concept, and species taxa are recognized as an emergent property of population-level processes. The tension between species concepts and diagnosis versus emergent recognition of species taxa is at least as old as Darwin, and is unlikely to be resolved soon in favor of either view, because the products of both approaches (discrete utilitarian taxon names for species, process-based understanding of the origins of differentiated metapopulations) continue to have important applications.

© 2010 The Author(s). *Evolution* © 2010 The Society for the Study of Evolution.
Evolution 65-3: 613–616

How Many Species Are There on Earth and in the Ocean?

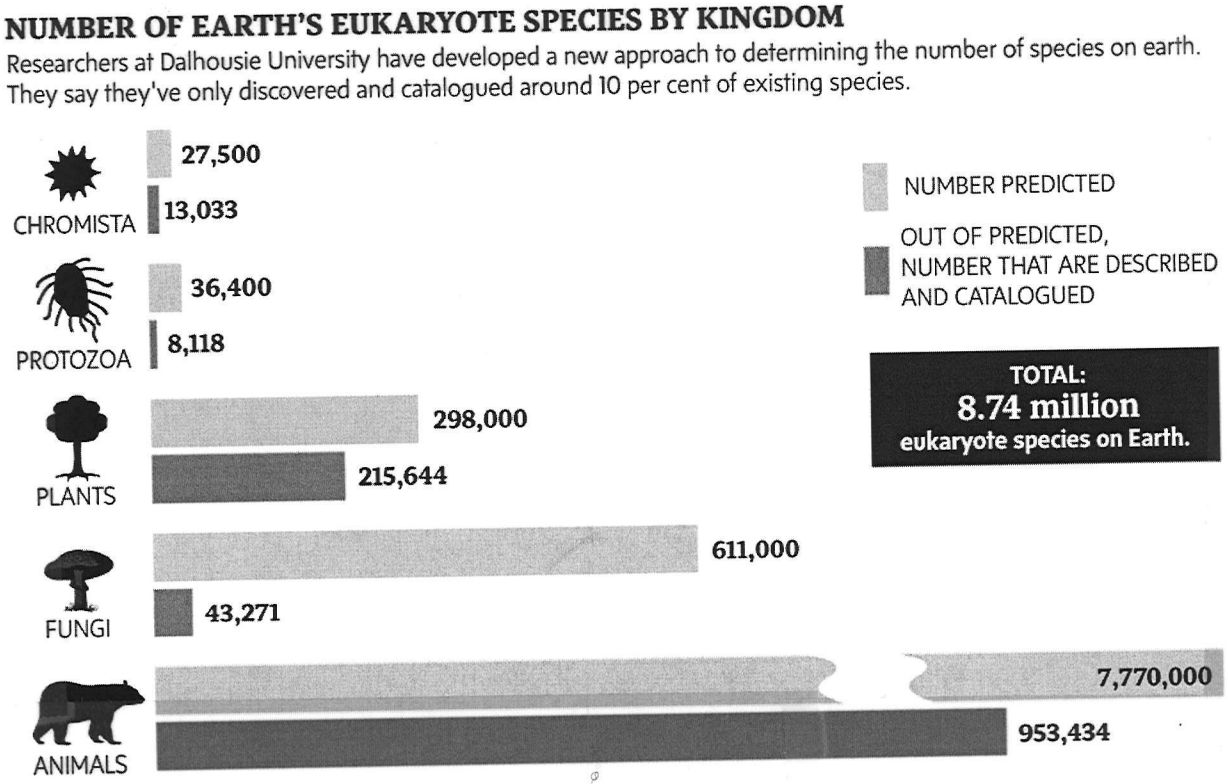
Camilo Mora[1,2]*, Derek P. Tittensor[1,3,4], Sina Adl[1], Alastair G. B. Simpson[1], Boris Worm[1]

1 Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, **2** Department of Geography, University of Hawaii, Honolulu, Hawaii, United States of America, **3** United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, United Kingdom, **4** Microsoft Research, Cambridge, United Kingdom

Abstract

The diversity of life is one of the most striking aspects of our planet; hence knowing how many species inhabit Earth is among the most fundamental questions in science. Yet the answer to this question remains enigmatic, as efforts to sample the world's biodiversity to date have been limited and thus have precluded direct quantification of global species richness, and because indirect estimates rely on assumptions that have proven highly controversial. Here we show that the higher taxonomic classification of species (i.e., the assignment of species to phylum, class, order, family, and genus) follows a consistent and predictable pattern from which the total number of species in a taxonomic group can be estimated. This approach was validated against well-known taxa, and when applied to all domains of life, it predicts ~8.7 million (±1.3 million SE) eukaryotic species globally, of which ~2.2 million (±0.18 million SE) are marine. In spite of 250 years of taxonomic classification and over 1.2 million species already catalogued in a central database, our results suggest that some 86% of existing species on Earth and 91% of species in the ocean still await description. Renewed interest in further exploration and taxonomy is required if this significant gap in our knowledge of life on Earth is to be closed.

Citation: Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How Many Species Are There on Earth and in the Ocean? PLoS Biol 9(8): e1001127. doi:10.1371/journal.pbio.1001127



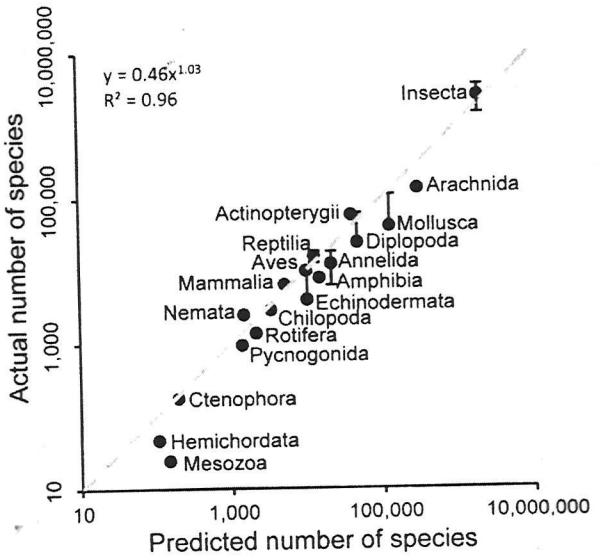


Figure 2. Validating the higher taxon approach. We compared the number of species estimated from the higher taxon approach implemented here to the known number of species in relatively well-studied taxonomic groups as derived from published sources [37]. We also used estimations from multimodel averaging from species accumulation curves for taxa with near-complete inventories. Vertical lines indicate the range of variation in the number of species from different sources. The dotted line indicates the 1:1 ratio. Note that published species numbers (*y*-axis values) are mostly derived from expert approximations for well-known groups; hence there is a possibility that those estimates are subject to biases arising from synonyms.
doi:10.1371/journal.pbio.1001127.g002

Citation: Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How Many Species Are There on Earth and in the Ocean? PLoS Biol 9(8): e1001127. doi:10.1371/journal.pbio.1001127

Species	Earth			Ocean		
	Catalogued	**Predicted**	**±SE**	**Catalogued**	**Predicted**	**±SE**
Eukaryotes						
Animalia	953,434	7,770,000	958,000	171,082	2,150,000	145,000
Chromista	13,033	27,500	30,500	4,859	7,400	9,640
Fungi	43,271	611,000	297,000	1,097	5,320	11,100
Plantae	215,644	298,000	8,200	8,600	16,600	9,130
Protozoa	8,118	36,400	6,690	8,118	36,400	6,690
Total	1,233,500	8,740,000	1,300,000	193,756	2,210,000	182,000
Prokaryotes						
Archaea	502	455	160	1	1	0
Bacteria	10,358	9,680	3,470	652	1,320	436
Total	10,860	10,100	3,630	653	1,320	436
Grand Total	**1,244,360**	**8,750,000**	**1,300,000**	**194,409**	**2,210,000**	**182,000**

Predictions for prokaryotes represent a lower bound because they do not consider undescribed higher taxa. For protozoa, the ocean database was substantially more complete than the database for the entire Earth so we only used the former to estimate the total number of species in this taxon. All predictions were rounded to three significant digits.

doi:10.1371/journal.pbio.1001127.t002

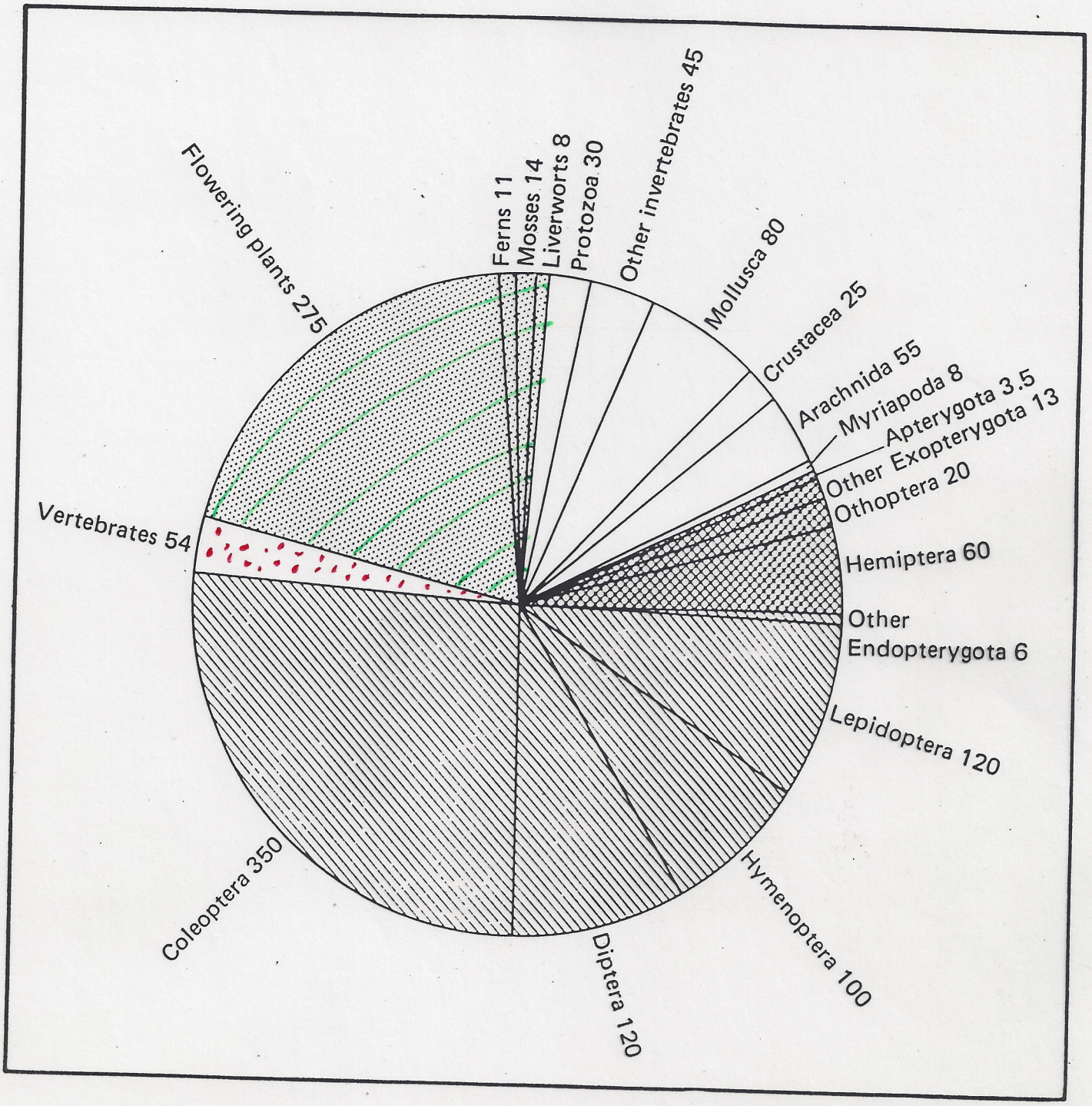


Figure 2–1
Relative size of the major groups of organisms on earth, exclusive of bacteria, fungi, and algae. Figures are in thousands. (T. R. E. Southwood, 1978, from "The components of diversity," *Symposia of the Royal Entomological Society of London*, no. 9, pp. 19–40, used with permission of Blackwell Scientific Publications, Ltd.)

V. COMPUTATION OF THE ENTROPY MEASURE OF SPECIE:

(See accompanying problem in text)

First Group of Birds

Species	p_i	log p_i	p_i log p_i
$i = 1$	0.2500	−1.3863	−0.346575
$i = 2$	0.2500	−1.3863	−0.346575
$i = 3$	0.2500	−1.3863	−0.346575
$i = 4$	0.2500	−1.3863	−0.346575
			−1.386300
			$H_s = 1.3863$

DIVERSITY (H_S) FOR TWO IMAGINARY GROUPINGS OF BIRD SPECIES

Second Group of Birds

Species	p_i	log p_i	p_i log p_i
$i = 1$	0.5000	−0.6932	−0.3466
$i = 2$	0.1250	−2.0794	−0.2599
$i = 3$	0.1250	−2.0794	−0.2599
$i = 4$	0.1250	−2.0794	−0.2599
$i = 5$	0.1250	−2.0794	−0.2599
			−1.3862
			$H_s = 1.3862$

Table 12.2 Some indices of species diversity. From Jennings and Reynolds (2000).

Index	Measures	Formula	Notes
Species richness (S)	Number of species	S	
Margalef (D)	Number of species for given number of individuals	$(S-1)/\ln N$	1
Menhinick's (D)	Number of species for given number of individuals	$S/\sqrt{N}$	
Shannon Wiener (H')	Richness and equitability	$-\Sigma p_i \ln p_i$	2
Eveness (for H')	Eveness	H'/H_{max} or $H'/\ln S$	
Brillouin (HB)	Richness and equitability	$(\ln N! - \Sigma \ln n_i)/N$	3
Pielou Eveness (for HB)	Eveness	HB/HB_{max}	
Simpsons (D)	Dominance	$\Sigma(n_i(n_i-1)/N(N-1))$	4
Hill N_0	Number of species	S	5
Hill N_1	Number of 'abundant' species	$\exp H'$	
Hill N_2	Number of 'very abundant' species	$1/D$	6
Taxonomic diversity (Δ)	Species diversity with taxonomic separation	$[\Sigma\Sigma_{i<j}\omega_{ij}x_i x_j]/[n(n-1)/2]$	7
Taxonomic distinctness (Δ^*)	Taxonomic distinctness without species diversity	$[\Sigma\Sigma_{i<j}\omega_{ij}x_i x_j]/[\Sigma\Sigma_{i<j}x_i x_j]$	7
Taxonomic distinctness (Δ^+)	Taxonomic distinctness for presence/absences data	$[\Sigma\Sigma_{i<j}\omega_{ij}]/[s(s-1)/2]$	7

Notes: (1) Where S = number of species and N = number of individuals. (2) Where p_i is the proportion of individuals of the ith species. Shannon–Weiner index assumes random sampling from an infinitely large population and that all species present are represented in the sample. In reality the true value of p_i is unknown and is estimated from $p_i = n_i/N$. (3) Alternative to Shannon–Wiener used to describe a known collection. The form appropriate to an infinitely large community would be Σp_i^2 where p_i is the proportion of individuals in the ith species. n is the number of individuals in the ith species. (4) Gives probability that any two species drawn at random from an infinitely large community belong to different species. Since D increases with decreasing diversity this index is often expressed as $1 - D$ or $1/D$. (5) Hill proposed a family of diversity measures ranging from those that emphasize uncommon species (richness) to those that emphasize dominance. N_0, N_1 and N_2 cover most aspects of diversity and are usually reported together. Note relationships between Hill numbers and the Shannon–Wiener and Simpson indices. (6) Where D is Simpson's Index. (7) x_i is abundance of ith of s species observed, $n = \Sigma_i x_i$ is total number of individuals in a sample, and ω_{ij} weights the path length linking species i and j through the taxonomy.

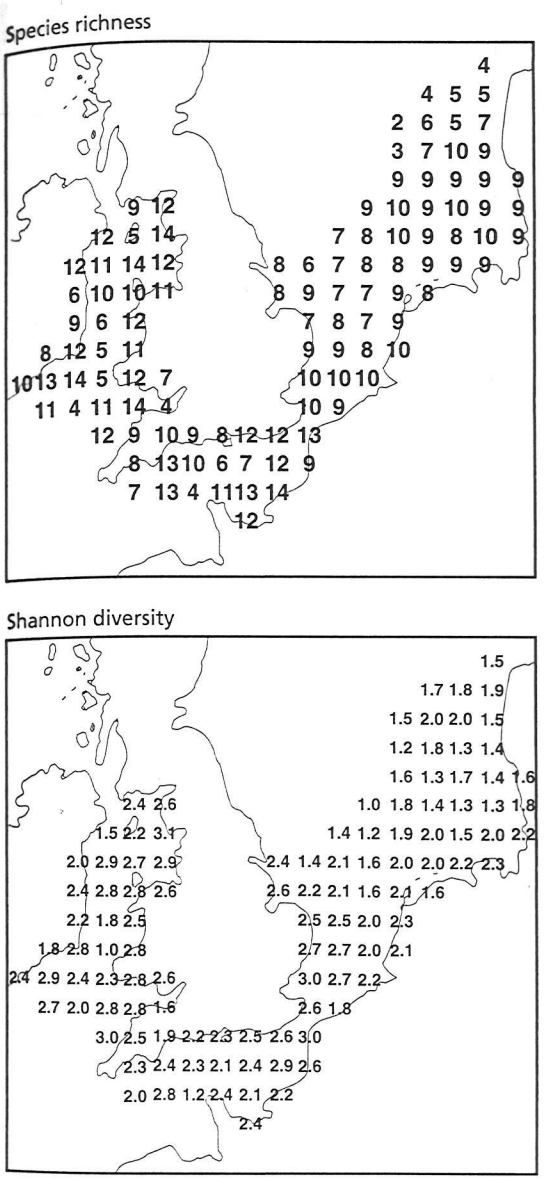


Fig. 12.8 Species richness of flatfish, and Shannon diversity in the seas around the British Isles. See Table 12.2 for a definition of these diversity indices. After Rogers *et al.* (1998).

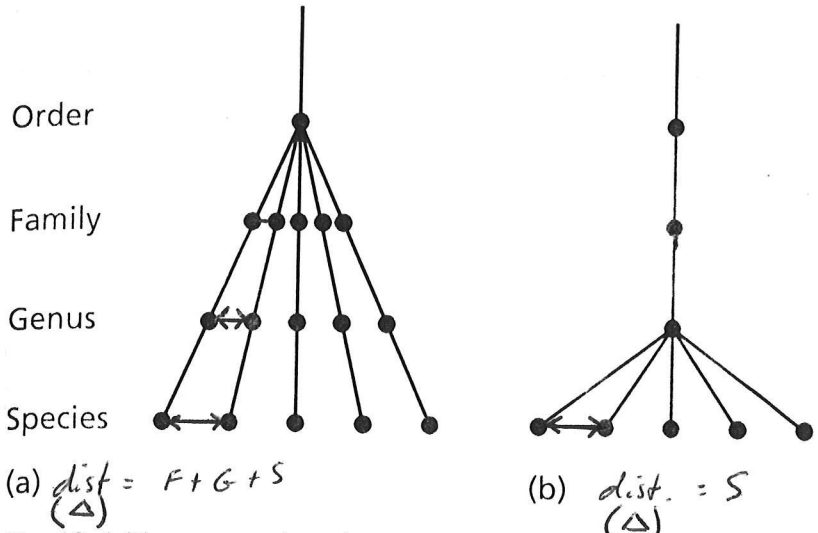


Fig. 12.4 Two examples of taxonomic hierarchies for species in samples. Mean taxonomic path lengths between individuals in (a) are greater than in (b). Thus sample (a) would be regarded as more diverse. After Clarke and Warwick (1998).

Vol. 351: 53–63, 2007
doi: 10.3354/meps07127

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 6

Surrogacy in natural patterns of benthic distribution and diversity: selected taxa versus lower taxonomic resolution

Maria Włodarska-Kowalczuk*, Monika Kędra

Institute of Oceanology PAS, Powstańców Warszawy 55, 81-712 Sopot, Poland

ABSTRACT: Surrogates are measures that reflect species-level community patterns, but can be more easily determined. The 2 main surrogacy methods (lowering the resolution of taxonomic identifications and selection of surrogate taxonomic groups) were first developed and widely tested in pollution impact studies. The performance of surrogates in natural benthic variability studies remains largely unexplored. The aim of the present study was to test both surrogacy methods (taxonomic sufficiency and selected taxa) in predicting benthic response (both diversity and distributional patterns) to a natural disturbance gradient produced by glacial sedimentation in an Arctic fjord. There was a strong correlation between benthic diversity and distribution patterns observed at the level of species, genus, and family. Little information was lost when the organisms were identified to the order level only. Additionally, polychaetes extracted from the basic dataset and analyzed separately were good predictors of variability throughout the macrobenthic community. The species distribution and diversity patterns observed along the glacial disturbance gradient did not persist when taxonomic resolution was lowered to the class or phylum level or when only molluscs or crustaceans were analyzed. Comparison of the current results to a number of other marine benthic studies shows that the taxonomic sufficiency of families is very high and consistent across different communities, habitats, and stress-generating factors; thus, families can be recommended as a reliable measure of benthic response to environmental gradients when species identifications are not available.

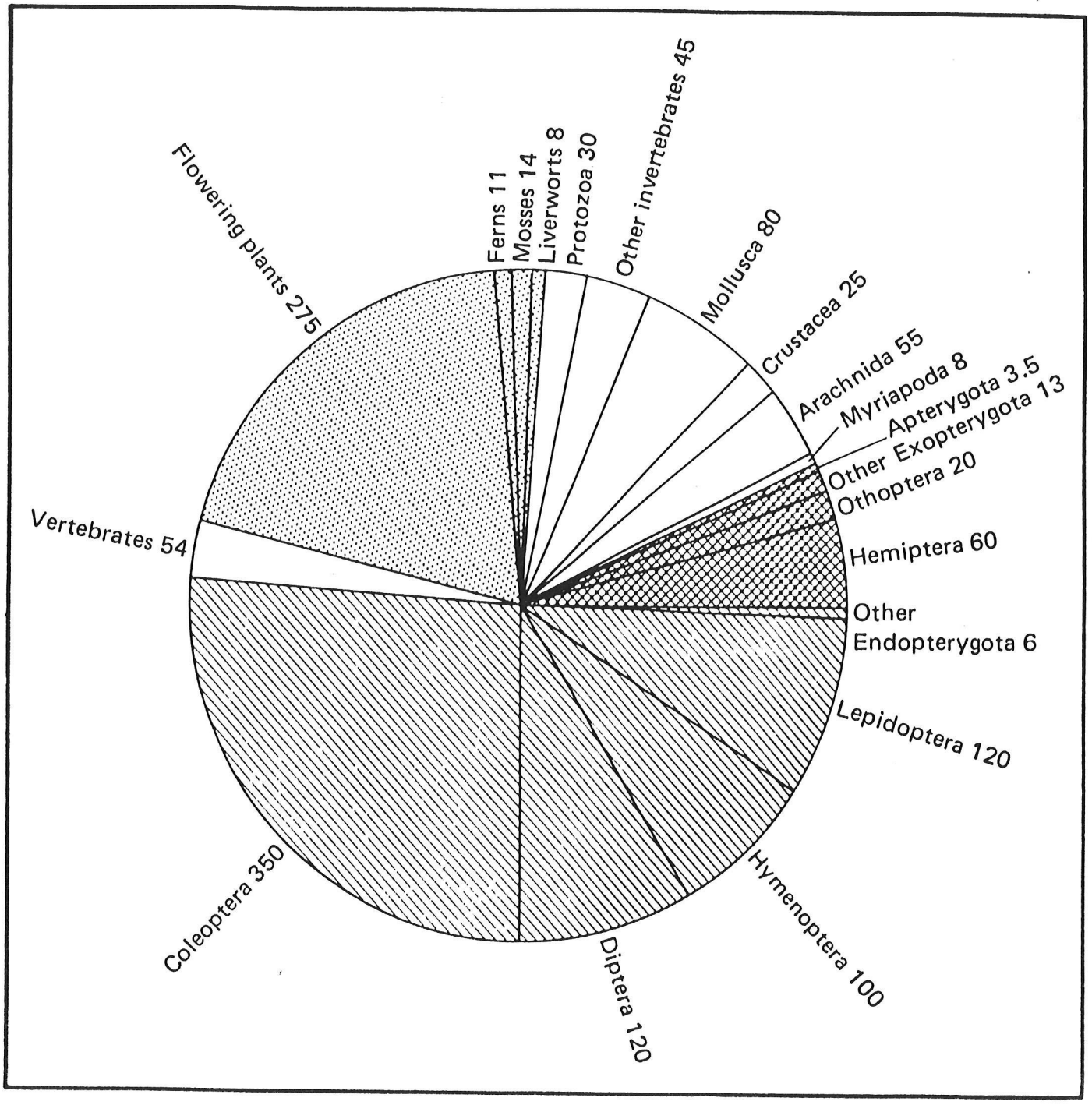


Figure 2–1
Relative size of the major groups of organisms on earth, exclusive of bacteria, fungi, and algae. Figures are in thousands. (T. R. E. Southwood, 1978, from "The components of diversity," *Symposia of the Royal Entomological Society of London,* no. 9, pp. 19–40, used with permission of Blackwell Scientific Publications, Ltd.)

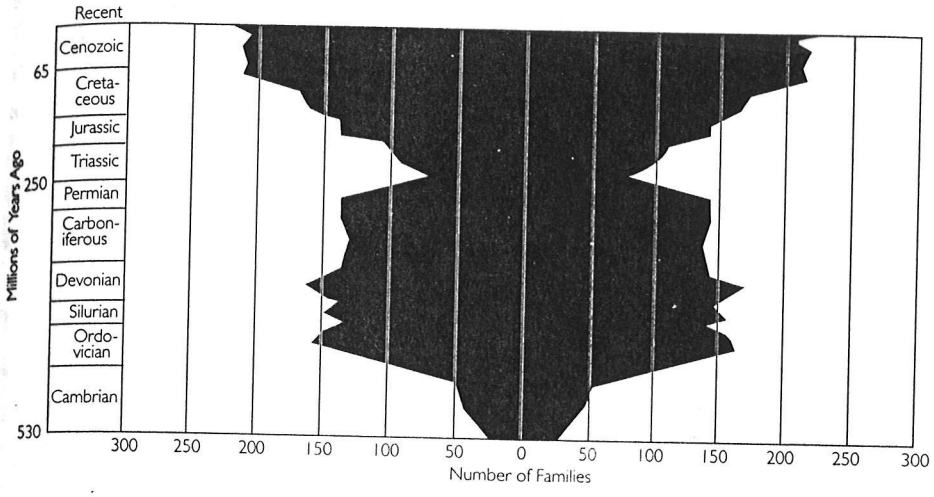


Figure 7.2 *Fluctuations in the number of families, and hence in the level of diversity, of well-skeletonized invertebrates living on the world's continental shelves during the past 530 million years are plotted by geological epoch in this graph. Time proceeds upward.*

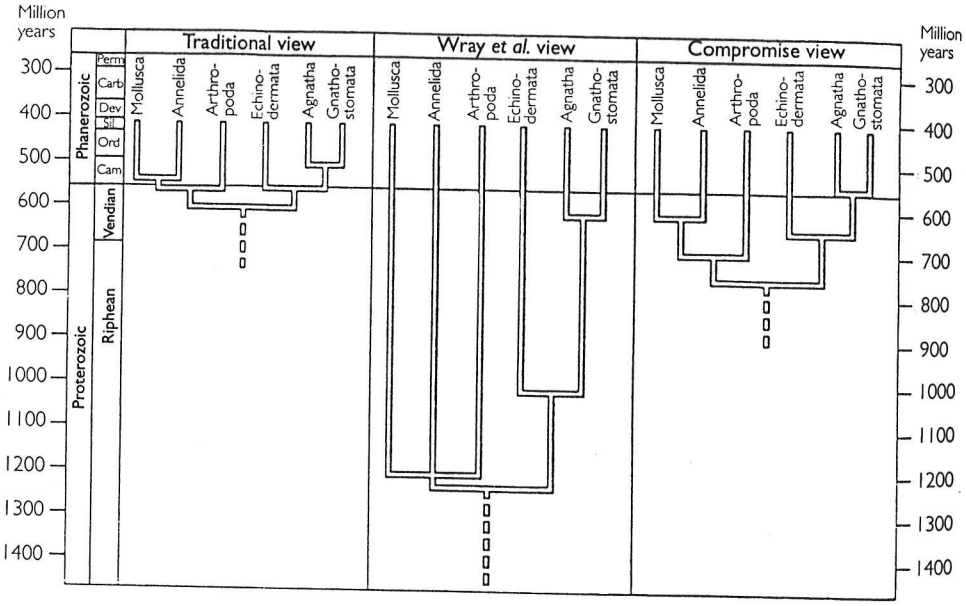


Figure 5.3 *Differing views of metazoan phylogeny. Most paleontologists follow the "traditional view" (left), accepting the fossil record as a fairly reliable indicator of original events. Molecular clocks are interpreted by Wray* et al. *(center) as indicating very deep origins for the principal metazoan phyla. The recognition that some molecular clocks run much faster than others suggests a "compromise view" (right), which implies that our search strategy for the first metazoans should be concentrated in the interval from about 750 million years onward. Perm, Permian; Carb, Carboniferous; Dev, Devonian; Sil, Silurian; Ord, Ordovician; Cam, Cambrian.*

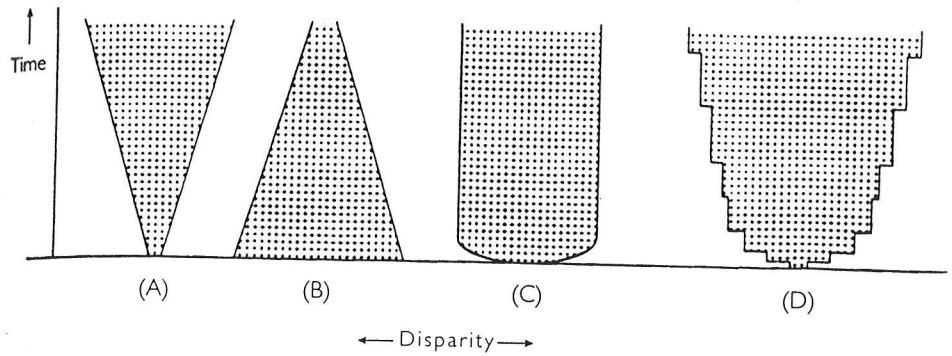


Figure 7.3 *Various interpretations of the history of life and its disparity. (A) The traditional view, whereby disparity steadily increases through geological time. (B) The view presented by S.J. Gould, whereby maximum disparity occurred in the Cambrian. (C) The view that disparity increased very rapidly in the Cambrian and thereafter stayed much the same. (D) The view that disparity increased rapidly in the Cambrian and since then has generally increased, though at varying rates. (From Simon Conway Morris.)*

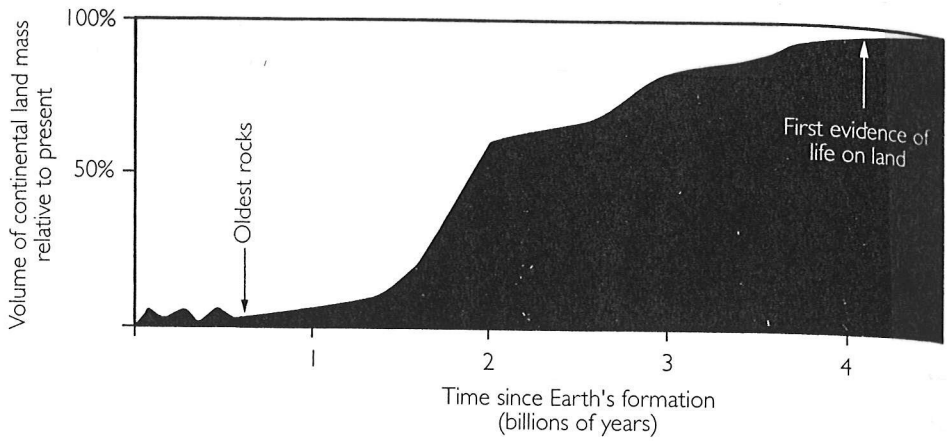
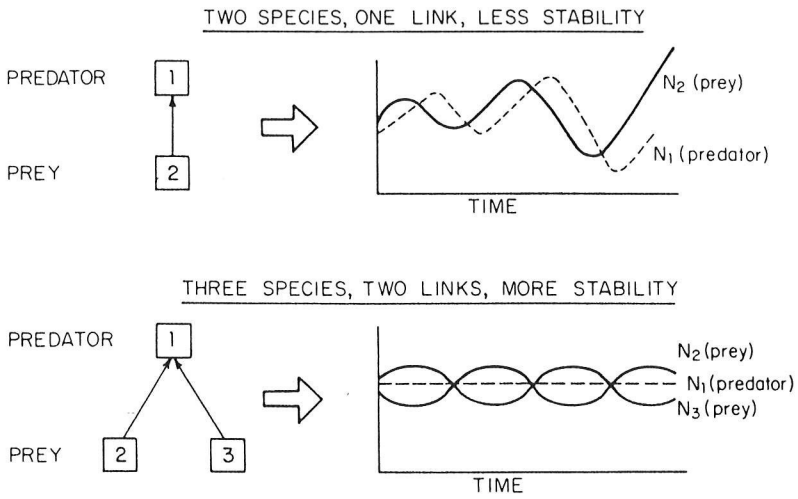
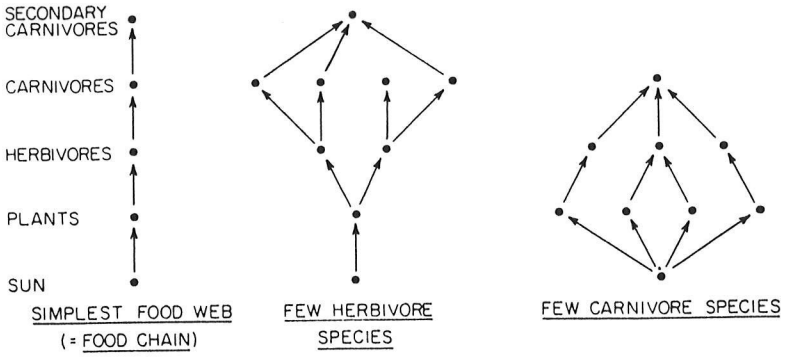
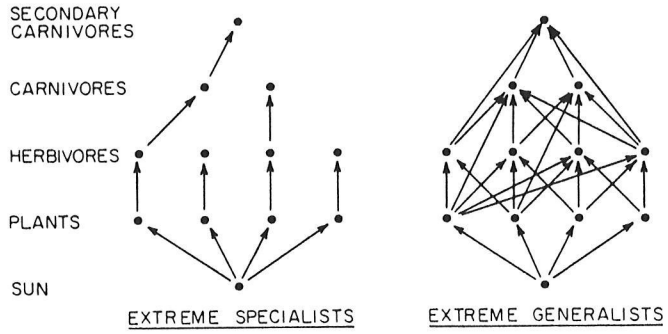


Figure 9.2 *Estimate of the growth of continental land mass with time (adapted from Taylor, 1999). For nearly a third of its history, Earth was a "water world" nearly devoid of land.*

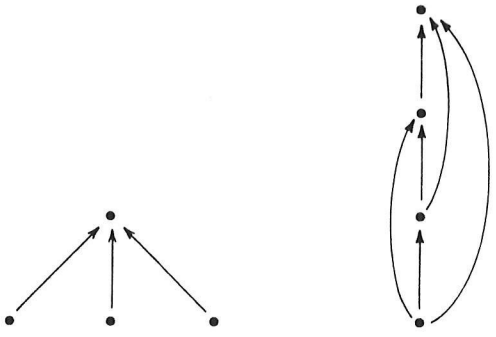


11 RELATIONSHIP BETWEEN SPECIES diversity and population stability. When a predator depends upon a single prey species, their populations can easily become unstable (*top*). But when two prey species are available, their independent fluctuations will tend to cancel out the fluctuations in the predator species (*bottom*).





12 FOOD WEBS, consisting of interconnected food chains, in the species communities of different ecosystems.



13 TWO FOOD WEBS in a community of four species. On the left, the least stable community with only three links. On the right, the most stable community with six links.

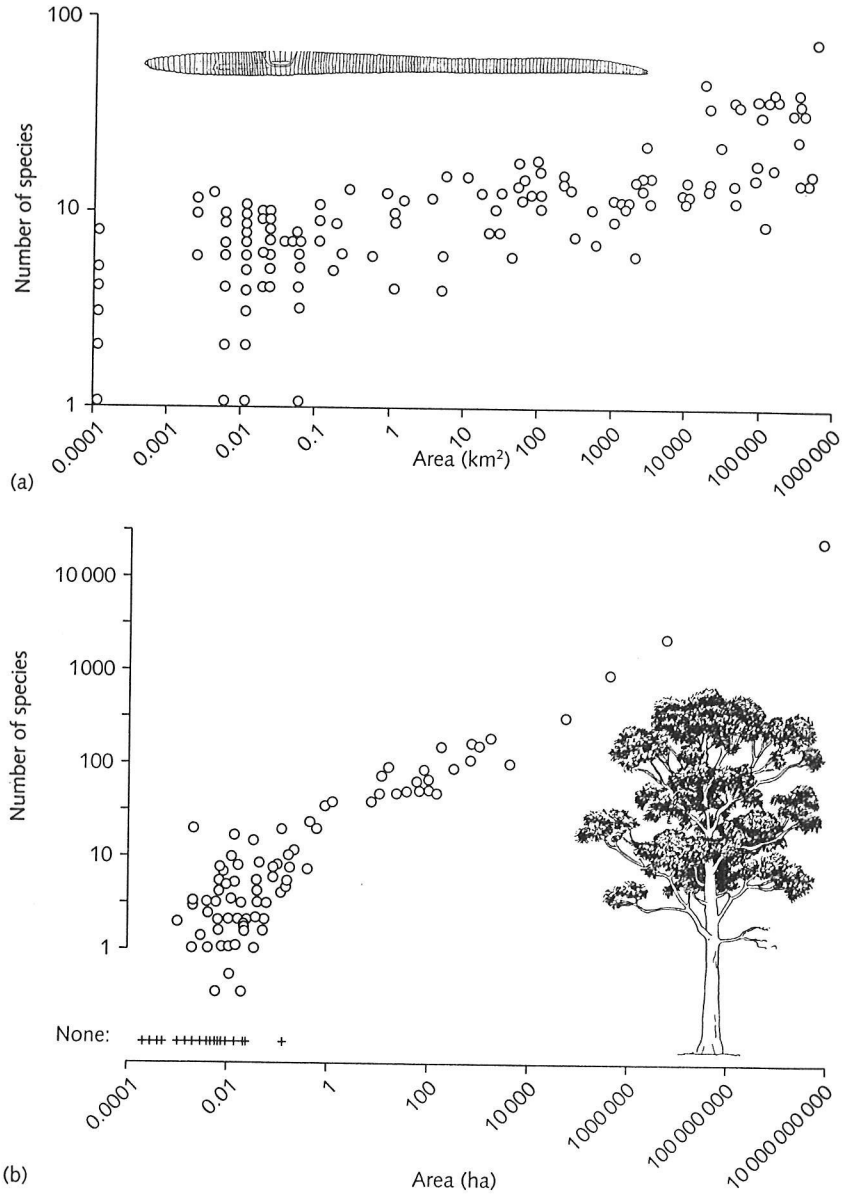


Figure 3.1 Species–area relationships for (a) lumbricid earthworms across Europe (from data in Judas 1988) and (b) plants on Australian islands. In both cases axes are logarithmically transformed. (After Rosenzweig 1995.)

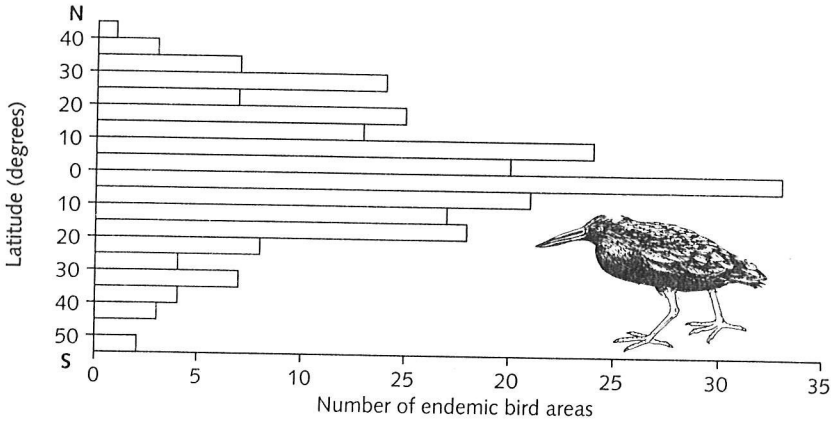


Figure 3.5 Latitudinal distribution of endemic bird areas (areas supporting two or more species with geographical ranges of < 50 000 km²). (After ICBP 1992.)

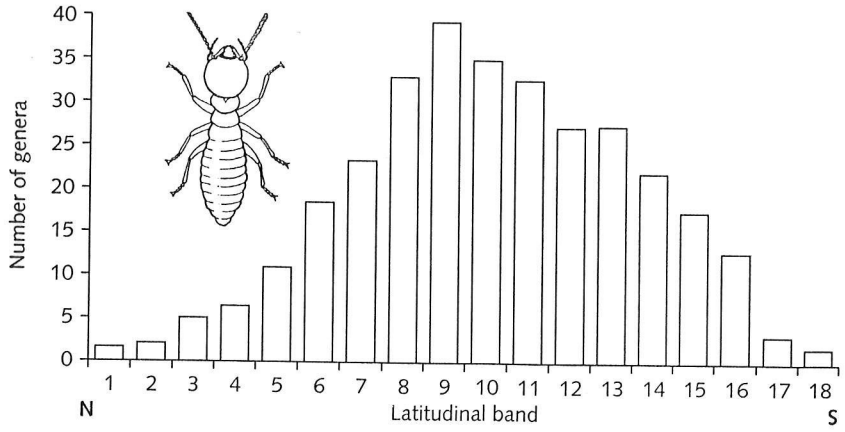


Figure 3.11 Mean generic richness of termites across areas (each of 611 000 km²) in different latitudinal bands (the equator lies at the junction of bands 9 and 10). (After Eggleton 1994.)

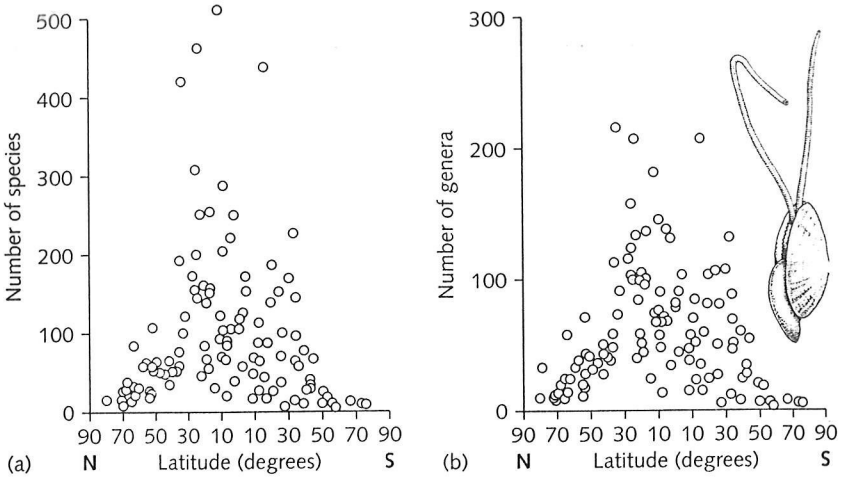


Figure 3.6 Latitudinal gradients in (a) the species and (b) the generic richness of marine bivalves in different localities. (After Flessa & Jablonski 1995.)

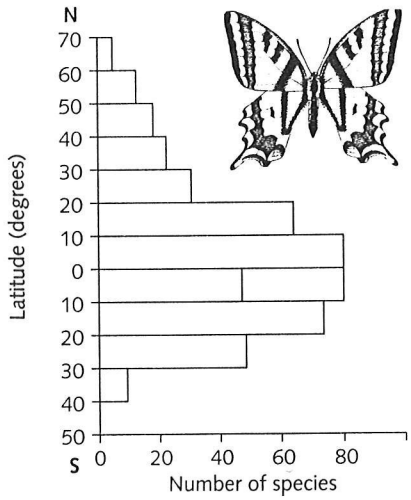


Figure 3.7 Latitudinal gradient in the species richness of swallowtail butterflies across the Americas. (After Sutton & Collins 1991.)

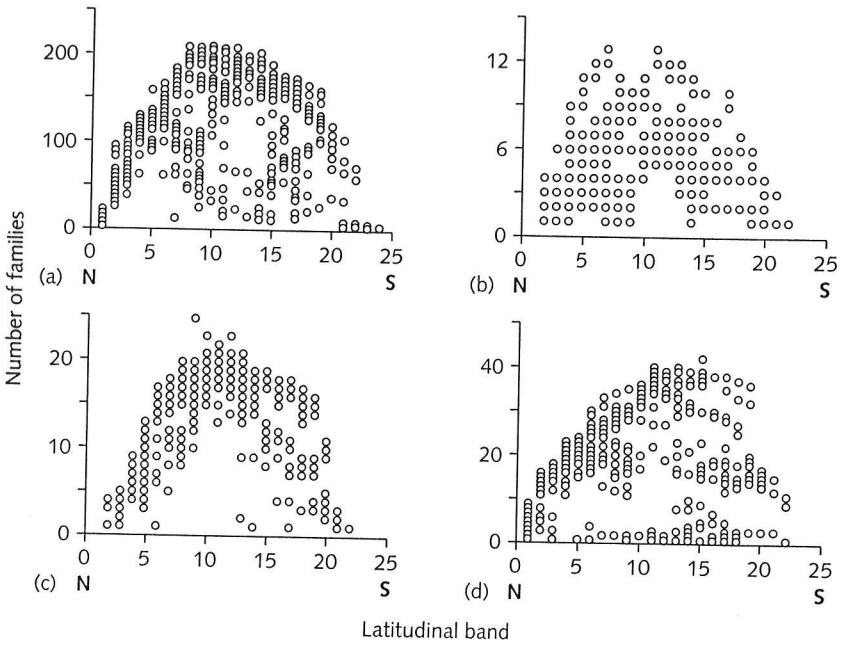


Figure 3.8 Latitudinal gradients in family richness for (a) seed plants, (b) amphibians, (c) reptiles and (d) mammals. Each data point represents the number of families in a cell of a grid of 611 000 km² squares; latitudinal bands run from north (1) to south (24) and the equator lies at the junction of bands 12 and 13. (After Gaston *et al.* 1995.)

Exception!

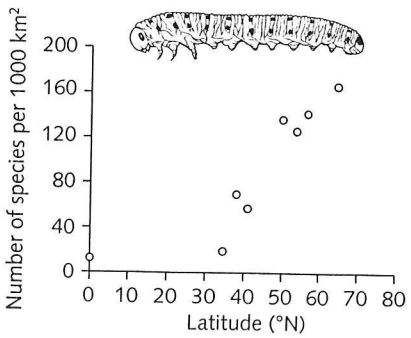


Figure 3.9 Latitudinal gradient in the species richness of sawflies. Each data point is the number of species per 1000 km² in a country or region. (After Kouki *et al.* 1994.)

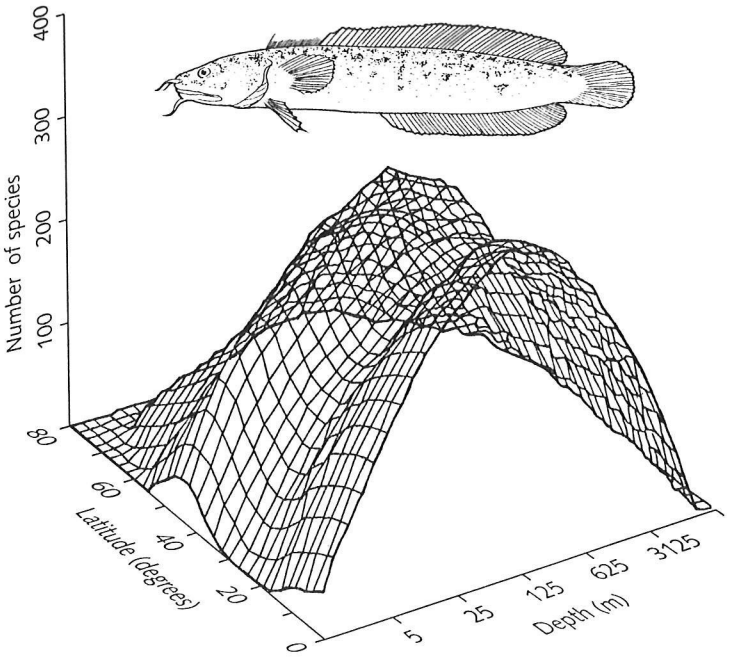


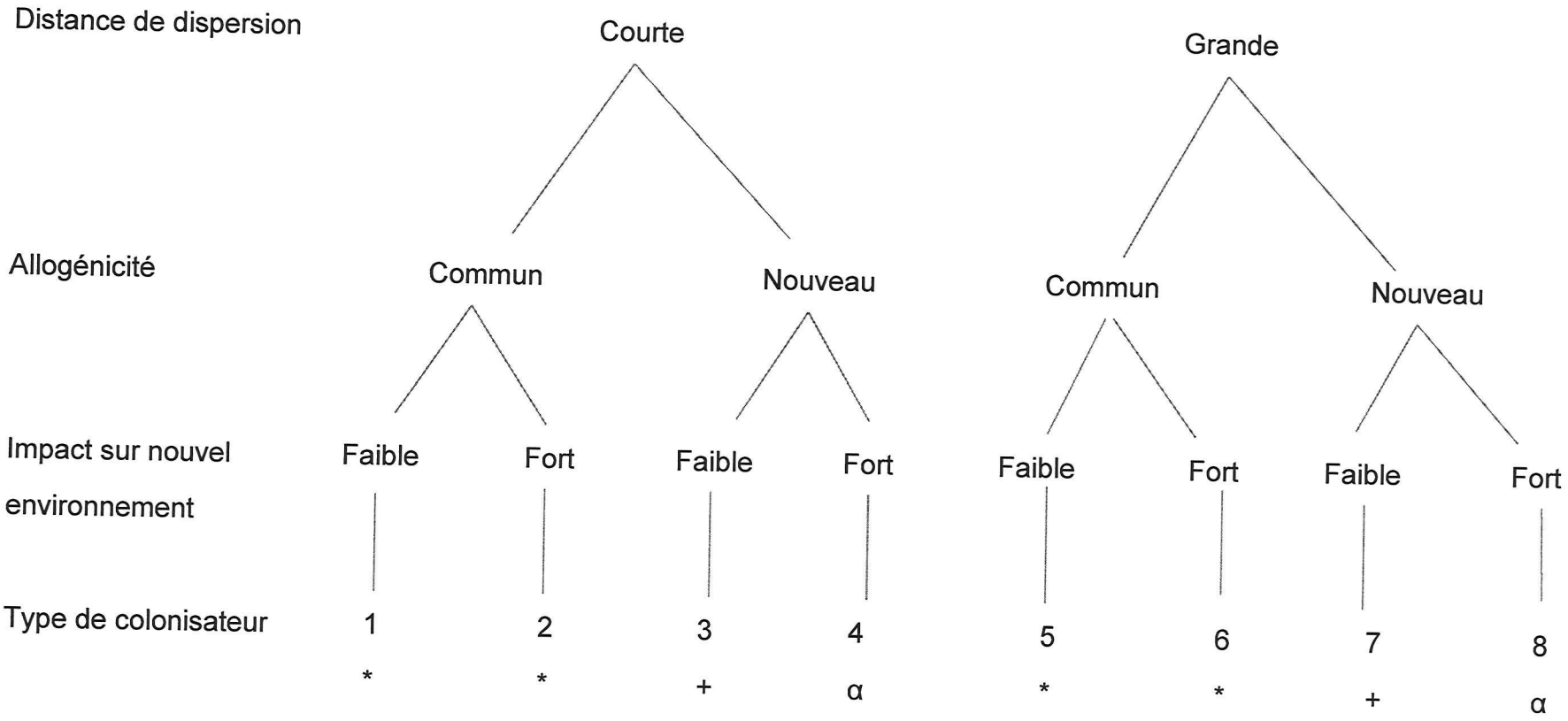
Figure 3.15 Three-dimensional relationship between species richness, latitude and depth for benthic fishes in the eastern Atlantic. (After Macpherson & Duarte 1994.)

Effects of Predator Hunting Mode on Grassland Ecosystem Function

Oswald J. Schmitz

The way predators control their prey populations is determined by the interplay between predator hunting mode and prey antipredator behavior. It is uncertain, however, how the effects of such interplay control ecosystem function. A 3-year experiment in grassland mesocosms revealed that actively hunting spiders reduced plant species diversity and enhanced aboveground net primary production and nitrogen mineralization rate, whereas sit-and-wait ambush spiders had opposite effects. These effects arise from the different responses to the two different predators by their grasshopper prey—the dominant herbivore species that controls plant species composition and accordingly ecosystem functioning. Predator hunting mode is thus a key functional trait that can help to explain variation in the nature of top-down control of ecosystems.

COLONISATION ET INVASION



* = colonisateurs successionaux

+ = colonisateurs nouveaux, non-invasifs

α = colonisateurs nouveaux, invasifs

Realistic Species Losses Disproportionately Reduce Grassland Resistance to Biological Invaders

Erika S. Zavaleta* and Kristin B. Hulvey

Consequences of progressive biodiversity declines depend on the functional roles of individual species and the order in which species are lost. Most studies of the biodiversity–ecosystem functioning relation tackle only the first of these factors. We used observed variation in grassland diversity to design an experimental test of how realistic species losses affect invasion resistance. Because entire plant functional groups disappeared faster than expected by chance, resistance declined dramatically with progressive species losses. Realistic biodiversity losses, even of rare species, can thus affect ecosystem processes far more than indicated by randomized-loss experiments.

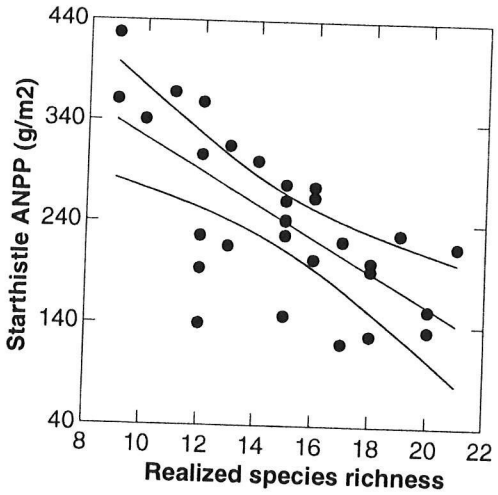


Fig. 2. The relation between realized species richness and starthistle aboveground net primary production (ANPP). Realized richness values reflect effects of negative (species that failed to establish) and positive (unplanted volunteers) deviations from treatment richness levels. Target diversity $F = 5.58$, $P = 0.002$, $R^2 = 0.59$; realized deviations $F = 7.85$, $P = 0.01$. 95% confidence limits are shown.

Vol. 342: 191–196, 2007 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published July 24

Propagule pressure of an invasive crab overwhelms native biotic resistance

A. L. Hollebone, M. E. Hay*

School of Biology, Georgia Institute of Technology, 311 Ferst Drive, Atlanta, Georgia 30332-0230, USA

ABSTRACT: Over the last decade, the porcelain crab *Petrolisthes armatus* invaded oyster reefs of Georgia, USA, at mean densities of up to 11 000 adults m^{-2}. Interactions affecting the invasion are undocumented. We tested the effects of native species richness and composition on invasibility by constructing isolated reef communities with 0, 2, or 4 of the most common native species, by seeding adult *P. armatus* into a subset of the 4 native species communities and by constructing communities with and without native, predatory mud crabs. At 4 wk, recruitment of *P. armatus* juveniles to oyster shells lacking native species was 2.75 times greater than to the 2 native species treatment and 3.75 times greater than to the 4 native species treatment. The biotic resistance produced by 2 species of native filter feeders may have occurred due to competition with, or predation on, the settling juveniles of the filter feeding invasive crab. Adding adult porcelain crabs to communities with 4 native species enhanced recruitment by a significant 3-fold, and countered the effects of native biotic resistance. Differences in recruitment at Week 4 were lost by Weeks 8 and 12, when densities of recent recruits reached ~17 000 to 34 000 crabs m^{-2} across all treatments. Thus, native species richness slows initial invasion, but early colonists stimulate settlement by later ones and produce tremendous propagule pressure that overwhelms the effects of biotic resistance.

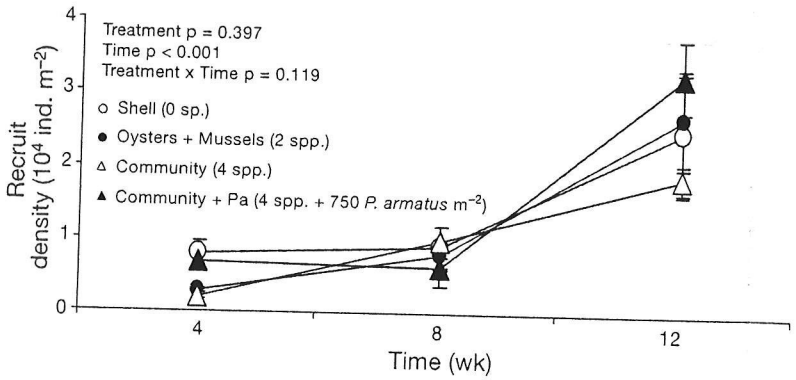


Fig. 2. *Petrolisthes armatus*. 2004 field experiment. Density (mean ± SE) of recruits over 12 wk in constructed oyster reefs that differed in species composition. p-values from repeated-measures ANOVA following transformation of data

Vol. 342: 127–138, 2007 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published July 24

Grazer-controlled recruitment of the introduced *Sargassum muticum* (Phaeophyceae, Fucales) in northern Europe

Kjersti Sjøtun[1,*], Sarah F. Eggereide[1,2], Tore Høisæter[1]

[1]University of Bergen, Department of Biology, PO Box 7800, 5020 Bergen, Norway

[2]*Present address:* Directorate of Fisheries, PO Box 2009, Nordnes, 5817 Bergen, Norway

ABSTRACT: *Sargassum muticum* (Yendo) Fensholt was introduced to European coasts during the 1970s. We studied survival and growth of seeded *S. muticum* germlings in field experiments on the southwestern coast of Norway, close to its present northernmost limit of distribution in Europe. A cage experiment was conducted twice (using different starting densities of germlings) at 2 localities during the summer and autumn of 2002, each experiment lasting 1 mo. Germling survival was significantly higher within grazer-excluding cages than on unprotected substrate. Germlings within cage controls (cages accessible to mesograzers) experienced intermediate mortality, which was nevertheless closer to that of unprotected than to cage-protected germlings. At a third locality, survival of unprotected germlings was recorded from September 2000 to February 2001, and only 0.6% of the germlings had survived by February. When relating proportion of mortality to initial density of germlings, we found no tendency of positive density-dependent mortality; on the contrary, on the substrate where grazers had access to the germlings, there was a tendency for high mortality when initial density was low and lower mortality when initial density was high. This suggests a 'swamping' effect of high germling densities on grazers. The growth of germlings during autumn and winter was very low compared with earlier reported measurements from Spain, and we suggest that relatively slow growth rates may make the germlings vulnerable to grazing impact. The results indicate that herbivorous grazing on early post-settlement stage germlings may be a limiting factor for the spread of *S. muticum* in southwestern Norway.

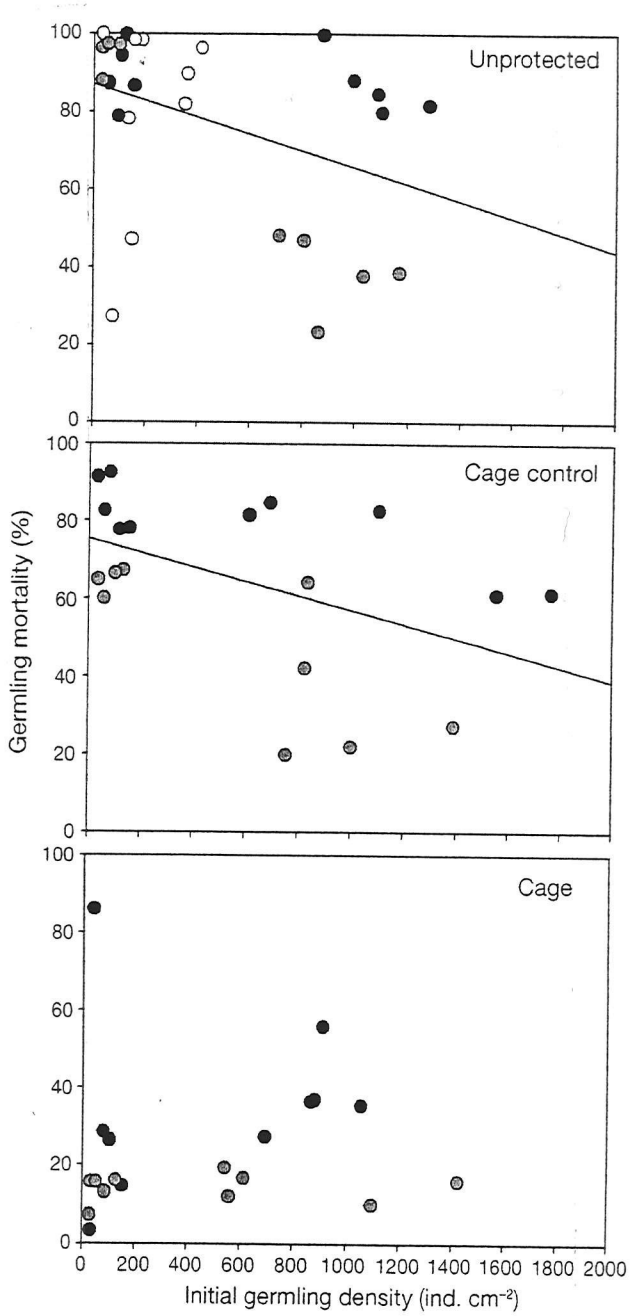


Fig. 2. *Sargassum muticum*. Proportional mortality of EPS germlings after 1 mo in relation to initial density (ind. cm^{-2}); all data from unprotected (upper plot), cage control (middle plot) and cage (lower plot) treatments at Sites A (○), B (●) and C (◉) shown. Regression line for data from unprotected (r^2 = 0.16) and for cage control treatment (r^2 = 0.22) shown

Mar Biol (2017) 164:185
DOI 10.1007/s00227-017-3202-1

SHORT NOTES

When the tiny help the mighty: facilitation between two introduced species, a solitary ascidian and a macroalga in northern Patagonia, Argentina

Patricio Javier Pereyra[1,2,3] · Paula de la Barra[1,2] · Marianela Gastaldi[2,3] · Juan Francisco Saad[2,3] · Fausto Nahuel Firstater[1,2,3] · Maite Andrea Narvarte[1,2,3]

Abstract Facilitation is recognized as one of the mechanisms by which nonnative species are integrated into new assemblages. The solitary ascidian *Styela clava* and the macroalga *Undaria pinnatifida* were introduced to San Antonio Bay, Argentina, with a couple of years of difference. We studied the occurrence pattern of both species in the area and tested the hypothesis that *S. clava* facilitates *U. pinnatifida* through a manipulative experiment. Our results clearly suggest a facilitation process between these species. The probability of finding *U. pinnatifida* is 30% higher in sites where *S. clava* is present and higher recruitment of *U. pinnatifida* occurred where *S. clava* is present than where it had been experimentally removed. Increased habitat complexity by the stalked ascidian *S. clava* can facilitate the establishment of *U. pinnatifida* by providing refugee from grazers, increasing surface for settlement, or providing greater access to light.

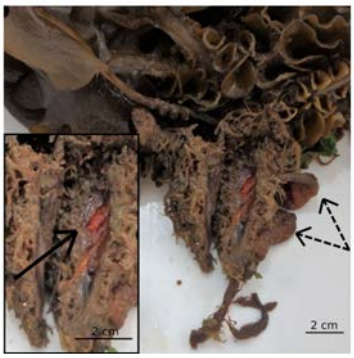


Fig. 4 *Undaria pinnatifida* overgrowing *Styela clava*. *Solid arrow* indicates the section of the stolon showing the basibiont completely covered; *dashed arrows* indicate two individuals of *S. clava* growing on the stolon of *U. pinnatifida*

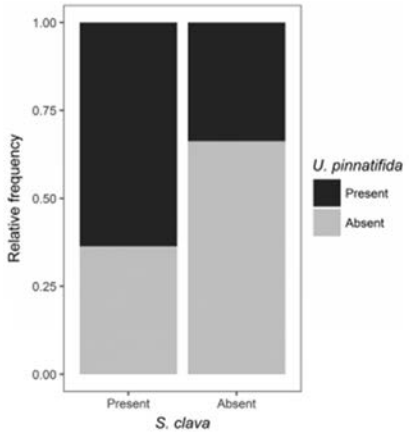


Fig. 2 Relative frequency of *Undaria pinnatifida* in quadrats where *Styela clava* was present ($n = 22$) and where *S. clava* was absent ($n = 71$)

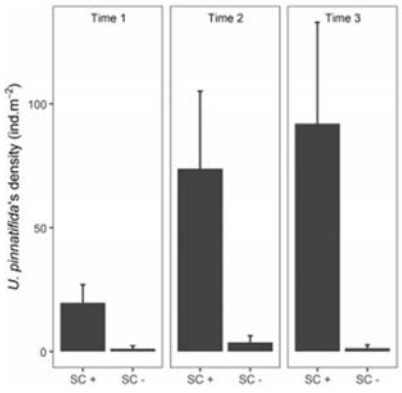


Fig. 3 Density of *Undaria pinnatifida* (mean ± SE) in plots with *Styella clava* (SC+) and plots where *S. clava* was removed (SC−). Time is expressed in months since the beginning of the experiment, where *1*, *2* and *3* represent June, July and August, respectively

In addition to the null hypothesis of no effect, there are four ways in which ecosystem processes might respond to reductions in species richness (Lawton 1994; Johnson *et al.* 1996).

1 The diversity–stability hypothesis predicts that ecological communities will decrease in ability to recover from disturbance and in energetic efficiency (productivity) as the number of species decreases (Fig. 4.1a; Johnson *et al.* 1996).

2 The rivet hypothesis likens the species in an ecosystem to the rivets holding together an aeroplane (Fig. 4.1b; Ehrlich & Ehrlich 1981). The loss of a few rivets may go unnoticed, because they may be redundant, but beyond some threshold losses will bring about catastrophic collapse. The relationship between species richness and ecosystem function will thus be non-linear, but may follow a variety of possible trajectories.

3 The redundant species hypothesis segregates species into functional groups, with ecosystem function being little impaired by species losses if representatives of all the groups remain but being markedly impaired if all the representatives of particular groups are lost; a minimal diversity is necessary for ecosystem function, but beyond this most species are redundant in their roles (Fig. 4.1c; Walker 1992).

4 The idiosyncratic response hypothesis suggests that as diversity changes so does ecosystem function, but the magnitude and direction of change is unpredictable because individual species have complex and varied roles (Fig. 4.1d; Lawton 1994).

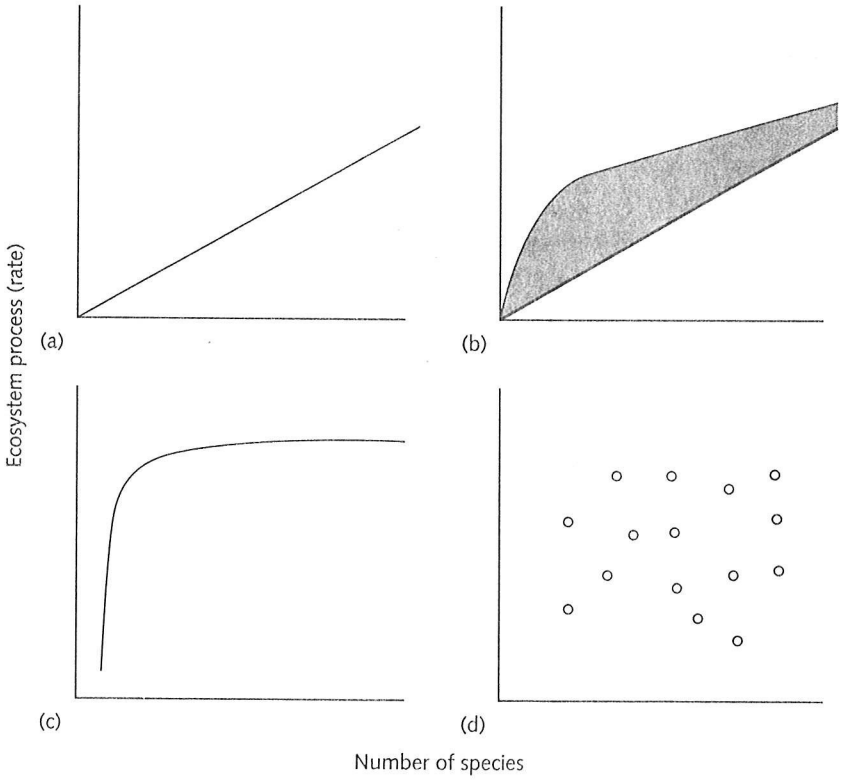


Figure 4.1 Possible relationships between ecosystem processes and the number of species in communities as predicted by (a) the diversity–stability hypothesis, (b) the rivet hypothesis, (c) the redundancy hypothesis and (d) the idiosyncratic hypothesis. (After Johnson *et al.* 1996.)

Annu. Rev. Ecol. Syst. 1999. 30:257–300
Copyright © 1999 by Annual Reviews. All rights reserved

THE RELATIONSHIP BETWEEN PRODUCTIVITY AND SPECIES RICHNESS

R. B. Waide[1], M. R. Willig[2], C. F. Steiner[3], G. Mittelbach[4], L. Gough[5], S. I. Dodson[6], G. P. Juday[7], and R. Parmenter[8]

Key Words primary productivity, biodiversity, functional groups, ecosystem processes

■ **Abstract** Recent overviews have suggested that the relationship between species richness and productivity (rate of conversion of resources to biomass per unit area per unit time) is unimodal (hump-shaped). Most agree that productivity affects species richness at large scales, but unanimity is less regarding underlying mechanisms. Recent studies have examined the possibility that variation in species richness within communities may influence productivity, leading to an exploration of the relative effect of alterations in species number per se as contrasted to the addition of productive species. Reviews of the literature concerning deserts, boreal forests, tropical forests, lakes, and wetlands lead to the conclusion that extant data are insufficient to conclusively resolve the relationship between diversity and productivity, or that patterns are variable with mechanisms equally varied and complex. A more comprehensive survey of the ecological literature uncovered approximately 200 relationships, of which 30% were unimodal, 26% were positive linear, 12% were negative linear, and 32% were not significant. Categorization of studies with respect to geographic extent, ecological extent, taxonomic hierarchy, or energetic basis of productivity similarly yielded a heterogeneous distribution of relationships. Theoretical and empirical approaches increasingly suggest scale-dependence in the relationship between species richness and productivity; consequently, synthetic understanding may be contingent on explicit considerations of scale in analytical studies of productivity and diversity.

PLANT ECOLOGY

Comment on “Worldwide evidence of a unimodal relationship between productivity and plant species richness”

Andrew T. Tredennick,[1]*† Peter B. Adler,[1]† James B. Grace,[2]† W. Stanley Harpole,[3]† Elizabeth T. Borer,[4]† Eric W. Seabloom,[4]† T. Michael Anderson,[5] Jonathan D. Bakker,[6] Lori A. Biederman,[7] Cynthia S. Brown,[8] Yvonne M. Buckley,[9] Chengjin Chu,[10] Scott L. Collins,[11] Michael J. Crawley,[12] Philip A. Fay,[13] Jennifer Firn,[14] Daniel S. Gruner,[15] Nicole Hagenah,[16] Yann Hautier,[17] Andy Hector,[18] Helmut Hillebrand,[19] Kevin Kirkman,[16] Johannes M. H. Knops,[20] Ramesh Laungani,[21] Eric M. Lind,[4] Andrew S. MacDougall,[22] Rebecca L. McCulley,[23] Charles E. Mitchell,[24] Joslin L Moore,[25] John W. Morgan,[26] John L. Orrock,[27] Pablo L. Peri,[28] Suzanne M. Prober,[29] Anita C. Risch,[30] Martin Schütz,[30] Karina L. Speziale,[31] Rachel J. Standish,[32] Lauren L. Sullivan,[4] Glenda M. Wardle,[33] Ryan J. Williams,[34] Louie H. Yang[35]

Fraser et al. (Reports, 17 July 2015, p. 302) report a unimodal relationship between productivity and species richness at regional and global scales, which they contrast with the results of Adler et al. (Reports, 23 September 2011, p. 1750). However, both data sets, when analyzed correctly, show clearly and consistently that productivity is a poor predictor of local species richness.

‘It is time to focus on effect sizes and variance explained rather than just P values.’

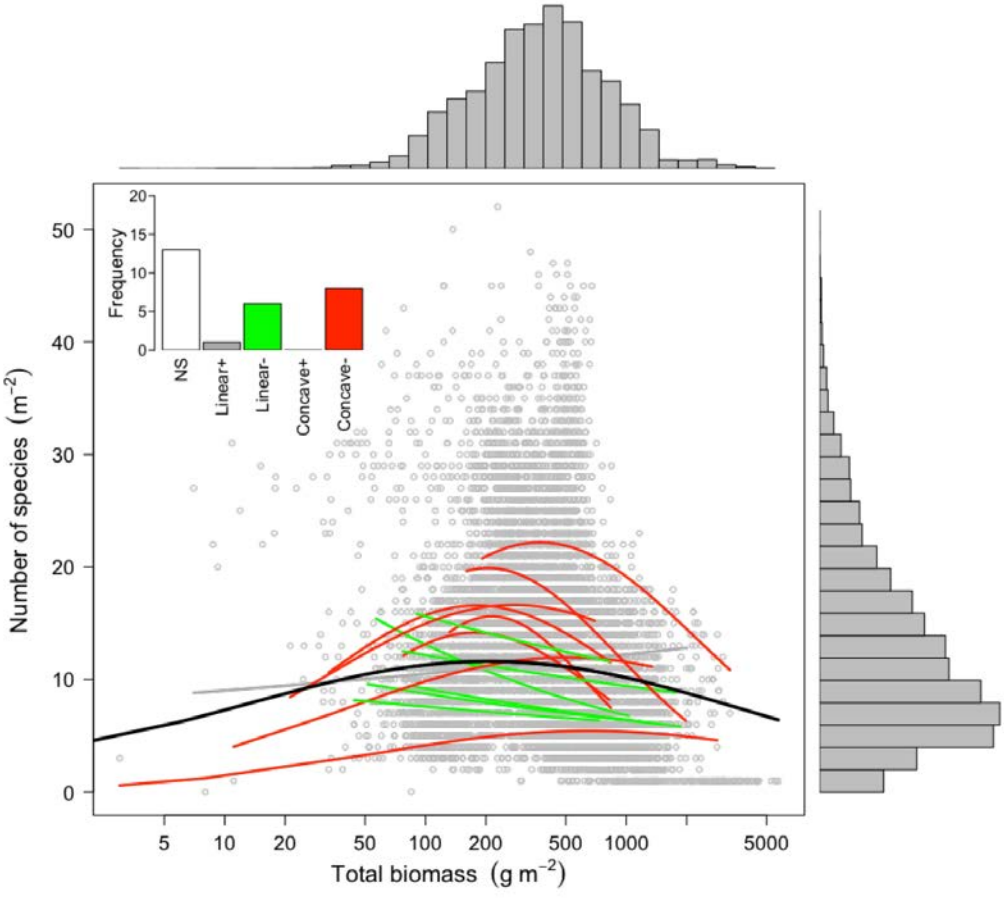


Fig. 1. Species richness as a function of biomass production at the site level (colored lines) and at the global extent (heavy black line).

.

Biodiversity loss and its impact on humanity

Bradley J. Cardinale[1], J. Emmett Duffy[2], Andrew Gonzalez[3], David U. Hooper[4], Charles Perrings[5], Patrick Venail[1], Anita Narwani[1], Georgina M. Mace[6], David Tilman[7], David A. Wardle[8], Ann P. Kinzig[5], Gretchen C. Daily[9], Michel Loreau[10], James B. Grace[11], Anne Larigauderie[12], Diane S. Srivastava[13] & Shahid Naeem[14]

Table 1 | Balance of evidence linking biodiversity to ecosystem services

Category of service	Measure of service provision	SPU	Diversity level	Source	Study type	*N*	Relationship	
							Predicted	Actual
Provisioning								
Crops	Crop yield	Plants	Genetic	DS	Exp	575	↘	↘
			Species	DS	Exp	100	↗	↗
Fisheries	Stability of fisheries yield	Fish	Species	PS	Obs	8	↘	↘
Wood	Wood production	Plants	Species	DS	Exp	53	↘	↘
Fodder	Fodder yield	Plants	Species	DS	Exp	271	↘	↘
Regulating								
Biocontrol	Control of herbivorous pests (bottom-up effect of plant diversity)	Plants	Species	DS*	Obs	40	↘	↘
		Plants	Species	DS†	Exp	100	↘	↘
		Plants	Species	DS‡	Exp	287	↗	↗
		Plants	Species	DS§	Exp	100	↘	↘
	Control of herbivorous pests (top-down effect of natural enemy diversity)	Natural enemies	Species/trait	DS*	Obs	18	■	■
		Natural enemies	Species	DS†	Exp/Obs	266	↘	↘
		Natural enemies	Species	DS‡	Exp	38	↘	↘
	Resistance to plant invasion	Plants	Species	DS	Exp	120	↗	↗
	Disease prevalence (on plants)	Plants	Species	DS	Exp	107	↘	↘
	Disease prevalence (on animals)	Multiple	Species	DS	Exp/Obs	45	↗	↗
Climate	Primary production	Plants	Species	DS	Exp	7	↘	■
	Carbon sequestration	Plants	Species	DS	Exp	479	↘	↘
	Carbon storage	Plants	Species/trait	PS	Obs	33	↗	↗
Soil	Soil nutrient mineralization	Plants	Species	DS	Exp	103	↘	↘
	Soil organic matter	Plants	Species	DS	Exp	85	↘	↘
Water	Freshwater purification	Multiple	Genetic/species	PS	Exp	8	↘	■
Pollination	Pollination	Insects	Species	PS	Obs	7	↗	↗

For each ecosystem service we searched the ISI Web of Knowledge for published data syntheses (DS). The footnote symbols in the 'Source' column refer to different syntheses. When a synthesis was not available, we completed our own primary search (PS; see Box 2). Detailed results are given in Supplementary Table 2. Data presented here are summarized as follows: green, actual data relationships agree with predictions; yellow, Data show mixed results; red, data conflict with predictions. Exp, experimental; *N*, number of data points; Obs, observed; SPU, service providing unit (where natural enemies include predators, parasitoids and pathogens). Note that 13 ecosystem services are not included in this table due to lack of data (<5 relationships, see Supplementary Table 2).

Marine Biology (2000) 137: 325–337

© Springer-Verlag 2000

L. O. Veale · A. S. Hill · S. J. Hawkins · A. R. Brand

Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats

Received: 29 January 2000 / Accepted: 31 May 2000

Abstract This paper examines spatial differences in the distribution of by-catch assemblages from the scallop [*Pecten maximus* (L.) and *Aequipecten opercularis* (L.)] fishing grounds in the North Irish Sea, during 1995. The sites examined have been exposed to differing known levels of fishing disturbance by scallop dredging, based on unusually high-resolution data extracted from fishermens' logbooks. Uni- and multi-variate techniques have been used on a production dataset (a value which incorporates both abundance and biomass figures), as well as abundance and biomass data individually. The original species list was reduced to higher taxonomic groupings in line with the theory that the latter is more appropriate for detecting anthropogenic change. Species diversity and richness, total number of species, and total number of individuals all decrease significantly with increasing fishing effort. Species dominance increases with effort. Total abundance, biomass and production, and the production of most of the major individual taxa investigated decrease significantly with increasing effort. Multivariate analysis reveals a significant relationship between fishing effort and by-catch assemblage structure. The taxa most responsible for the differences are the echinoids and cnidarians, but prosobranch molluscs and crustaceans also contribute to the differences. By-catch assemblage structure is more closely related to fishing effort than any other environmental parameter investigated, including depth and sediment type. We observed an approximately linear decrease in diversity with increasing fishing disturbance, and suggest this is primarily due to selective removal of sensitive species and, more importantly, habitat homogenisation. These results were interpreted in the light of ecological theories relating disturbance to community structure. The argument that invertebrate scavenger populations benefit from prolonged exposure to fishing disturbance was also examined, but no supporting evidence was found.

Table 4 Spearmans rank-correlation coefficients(r) and significance value (p) between abundance, biomass and production of individual aggregated taxa and long-term fishing effort. Results are also given for total values and for biomass of colonial and reef-formizng species

Taxon	Abundance		Biomass		Production	
	r	p	r	p	r	p
Asteroidea	−0.37	< 0.05	−0.55	< 0.01	−0.52	< 0.01
Bivalvia	−0.57	< 0.01	−0.35	< 0.05	−0.43	< 0.01
Cnidaria	−0.41	< 0.05	−0.47	< 0.01	−0.46	< 0.01
Crustacea	−0.47	< 0.01	−0.33	< 0.05	−0.35	< 0.05
Echinoidea	−0.54	< 0.01	−0.39	< 0.05	−0.4	< 0.05
Prosobranchia	−0.37	< 0.05	−0.24	ns	−0.3	ns
Colonial species	–	–	−0.44	< 0.01	–	–
Total	−0.66	< 0.01	−0.54	< 0.01	−0.58	< 0.01

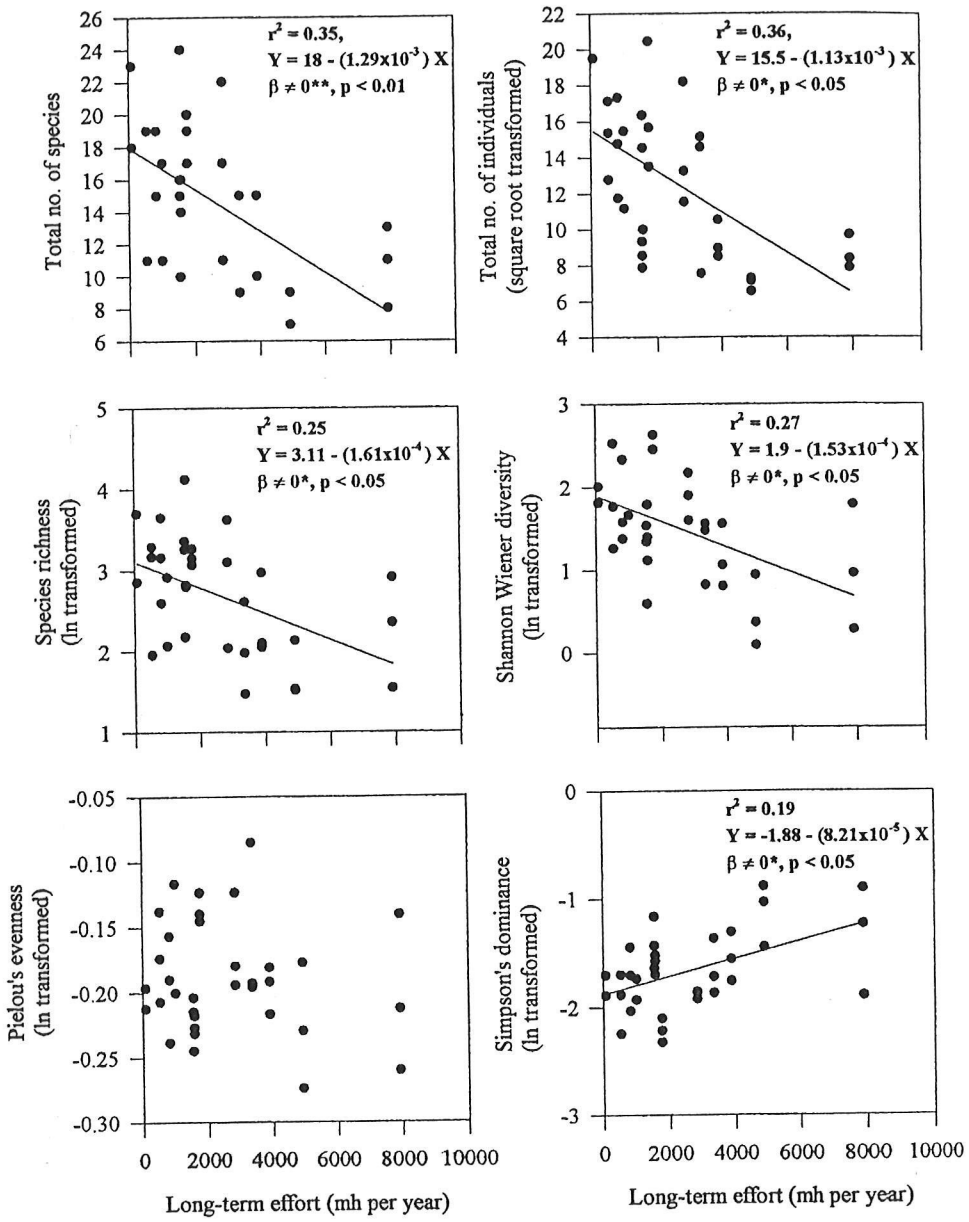


Fig. 2 Scatterplots of univariate community indices against long-term fishing effort (mh yr^{-1}), with linear regression line and equation. β (slope) is tested against zero, and r^2 is coefficient of determination

ELSEVIER

Journal of Experimental Marine Biology and Ecology 344 (2007) 23–34

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon

Mark A. Hixon [a,*], Brian N. Tissot [b]

[a] *Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, Oregon 97331-2914, USA*

[b] *Program in Environmental Science and Regional Planning, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, Washington 98686-9600 USA*

Abstract

We report the first quantitative comparison of trawled vs untrawled mud seafloor communities off the west coast of North America. Using a manned submersible, we ran visual transects at Coquille Bank, 25 km off the central coast of Oregon, USA, including six half-hour (mean length 1184 m) transects over mud seafloors 183–361 m deep. The shallowest transects were untrawled, whereas deeper transects were heavily trawled, as evidenced by extensive trawl-door tracks. Differences between trawled and untrawled seafloor assemblages were striking. We observed 23% more fish over untrawled compared to trawled seafloors, and recorded 27 fish species on untrawled bottoms, but only 19 species on trawled seafloors. Regarding benthic invertebrates, density of individuals was 6 times greater on untrawled compared to trawled bottoms. Nonetheless, we observed 11 taxa on trawled seafloors and only 6 taxa on untrawled bottoms. Principal components analysis (PCA) defined the untrawled assemblage as characterized by sea pens, ratfish, sablefish, ronquil, slender sole, and poacher. PCA defined the trawled assemblage as characterized by seastars, hermit crabs, bigfin eelpout, Dover sole, hagfish, and shortspine thornyhead. In untrawled areas, there was no correlation between sea-pen density and total fish density, whereas in trawled areas, there was a marginally inverse correlation between the density of trawl-door tracks and total fish density. The dominant fishes and macroinvertebrates on trawled seafloors are known mobile scavengers that may aggregate along trawl-door tracks. Sea pens that dominated untrawled bottoms are sessile, slow-growing, long-lived species that are likely to recover slowly from physical disturbance. We conclude that the observed differences between trawled and untrawled communities were the result of groundfishing activities rather than local environmental differences. Given that habitat considerations for groundfish management in this region focus exclusively on rocky seafloors, it seems prudent to consider the adverse effects of bottom trawling on mud seafloor ecosystems of the continental shelf and slope.

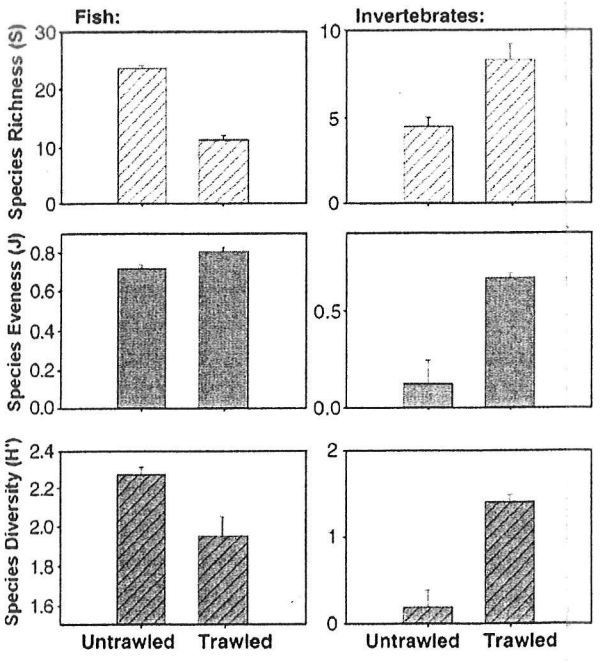


Fig. 4. Species diversity indices (mean+1 SE) for fishes and macroinvertebrates in untrawled and trawled areas adjacent to Coquille Bank, Oregon.

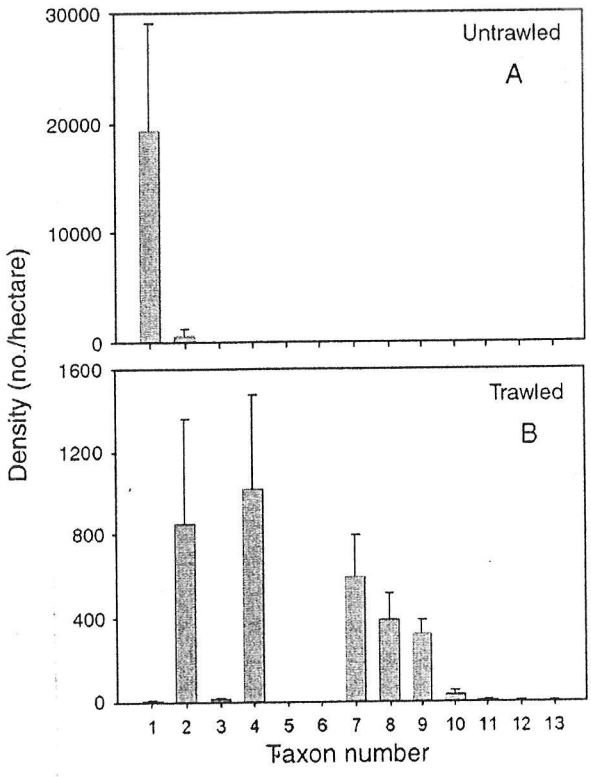


Fig. 5. Density of epibenthic macroinvertebrates (mean number per hectare+1 SE) in (A) untrawled and (B) trawled mud areas adjacent to Coquille Bank, Oregon. Taxon numbers are identified in Table 1. Sample sizes: untrawled area = two 30-minute transects; trawled area = four 30-minute transects. Note difference in *y*-axis scaling.

Marine Biology (2006) 149: 1489–1497
DOI 10.1007/s00227-006-0289-1

RESEARCH ARTICLE

Jennifer Griffiths · Megan N. Dethier · Amanda Newsom
James E. Byers · John J. Meyer · Fernanda Oyarzun
Hunter Lenihan

Invertebrate community responses to recreational clam digging

Received: 27 April 2005 / Accepted: 10 January 2006 / Published online: 5 May 2006
© Springer-Verlag 2006

Abstract Marine reserves can help in maintaining biodiversity and potentially be useful as a fishery management tool by removing human-mediated impacts. Intertidal, soft-sediment habitats can often support robust recreational and commercial shellfish harvests, especially for clams; however, there is limited research on the effects of reserves in these habitats. In San Juan County, Washington, several reserves prohibit recreational clam digging. We examined the effects of these reserves on infaunal community composition through comparison with non-reserve beaches during a 6-week period. Clam abundance, overall species richness and total polychaete family richness were greater on reserve beaches compared to non-reserve beaches. Additionally, an experiment within a reserve demonstrated negative impacts of digging on non-target infauna. These effects probably resulted from local disruption and disturbance of the sediment habitat and not from increased post-digging predation, which was controlled. Intertidal reserves could play an important role in sustaining local and potentially regional biodiversity.

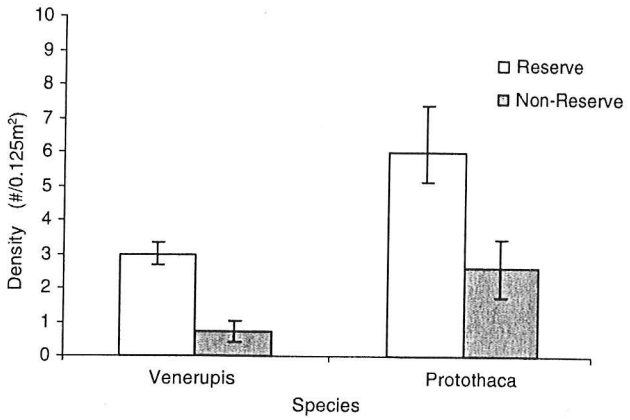


Fig. 3 *Protothaca* and *Venerupis* clam densities at reserve ($n=3$) and non-reserve ($n=6$) sites. Densities for each were averaged for both high and low tidal elevations. Bars represent ±1 SE

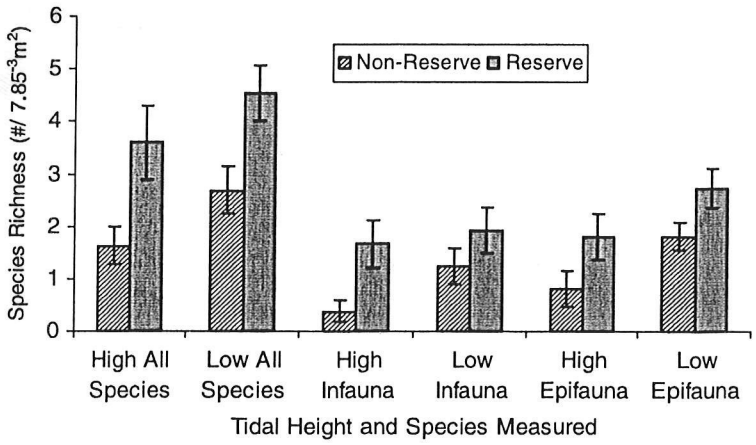


Fig. 4 Average non-clam species richness: reserves vs. non-reserve sites. Species density per core pooling all reserve sites and non-reserve sites by tidal height. Bars as in Fig. 3

Table 5.1 The pattern of human disturbance amongst biomes. Undisturbed areas have a record of primary vegetation and no evidence of disturbance, combined with a very low human population density. Partially disturbed areas have a record of shifting or extensive agriculture, evidence of secondary vegetation, livestock over carrying capacity or other evidence of human disturbance. Human dominated areas have a record of permanent agriculture or urban settlement, removal of primary vegetation or record of desertification or other permanent degradation. (After Hannah *et al.* 1995.)

Biome	Total area (km^2)	Area undisturbed (%)	Area partially disturbed (%)	Area human dominated (%)
Temperate broadleaf forests	9 519 442	6.1	12.0	81.9
Evergreen sclerophyllous forests	6 559 728	6.4	25.8	67.8
Temperate grasslands	12 074 494	27.6	32.0	40.4
Subtropical and temperate rainforests	4 232 299	33.0	20.9	46.1
Tropical dry forests	19 456 659	30.5	41.1	45.9
Mixed mountain systems	12 133 746	29.3	45.0	25.6
Mixed island systems	3 256 096	46.6	11.6	41.8
Cold deserts/semi-deserts	10 930 762	45.4	46.1	8.5
Warm deserts/semi-deserts	29 242 021	55.8	32.0	12.2
Tropical humid forests	11 812 012	63.2	11.9	24.9
Tropical grasslands	4 797 090	74.0	21.3	4.7
Temperate needleleaf forests	18 830 709	81.7	6.4	11.8
Tundra and Arctic desert	20 637 953	99.3	0.7	0.3

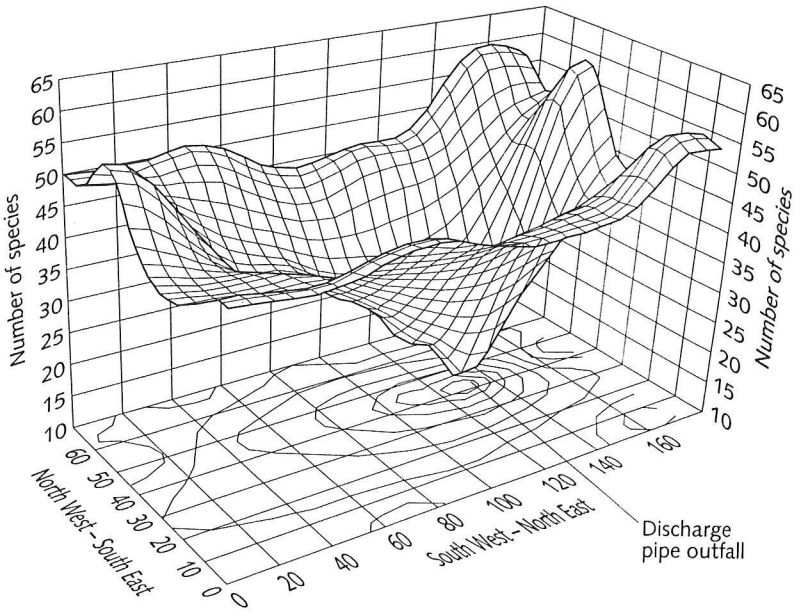


Figure 3.19 A three-dimensional plot showing the depression of the numbers of microscopic sediment-dwelling species of meiofauna associated with an industrial effluent discharged to the outer reaches of a British estuary. The area shown is approximately 1.7 × 1.7 km. (After Anon. 1994.)

Impact of Nitrogen Deposition on the Species Richness of Grasslands

Carly J. Stevens,[1,2*] Nancy B. Dise,[1,3] J. Owen Mountford,[2] David J. Gowing[4]

A transect of 68 acid grasslands across Great Britain, covering the lower range of ambient annual nitrogen deposition in the industrialized world (5 to 35 kg N ha^{-1} $year^{-1}$), indicates that long-term, chronic nitrogen deposition has significantly reduced plant species richness. Species richness declines as a linear function of the rate of inorganic nitrogen deposition, with a reduction of one species per 4-m^2 quadrat for every 2.5 kg N ha^{-1} $year^{-1}$ of chronic nitrogen deposition. Species adapted to infertile conditions are systematically reduced at high nitrogen deposition. At the mean chronic nitrogen deposition rate of central Europe (17 kg N ha^{-1} $year^{-1}$), there is a 23% species reduction compared with grasslands receiving the lowest levels of nitrogen deposition.

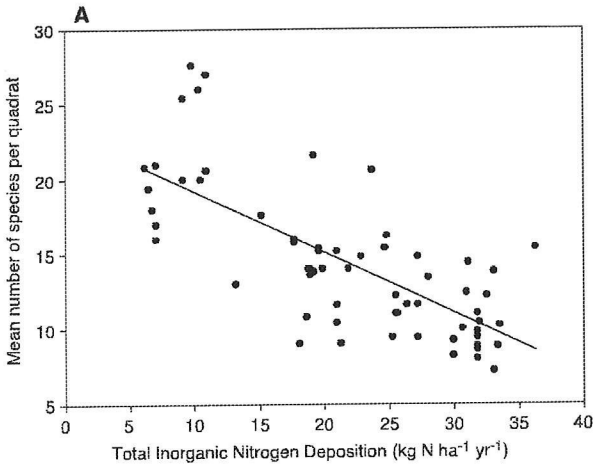


Fig. 2. (**A**) Acid grassland species richness plotted against N deposition for 68 field sites visited in the summers of 2002 and 2003. The regression line shown is Eq. 1. (**B**) Plant species richness versus N deposition and topsoil pH. The regression equation shown is: *Plant Species Richness* = 6.63 + 3.40(*Top pH*) − 0.316(*Nin*); $r^2 = 0.61$, $N = 68$, $P < 0.004$.

REVIEW

Historical Overfishing and the Recent Collapse of Coastal Ecosystems

Jeremy B. C. Jackson,[1,2*] Michael X. Kirby,[3] Wolfgang H. Berger,[1] Karen A. Bjorndal,[4] Louis W. Botsford,[5] Bruce J. Bourque,[6] Roger H. Bradbury,[7] Richard Cooke,[2] Jon Erlandson,[8] James A. Estes,[9] Terence P. Hughes,[10] Susan Kidwell,[11] Carina B. Lange,[1] Hunter S. Lenihan,[12] John M. Pandolfi,[13] Charles H. Peterson,[12] Robert S. Steneck,[14] Mia J. Tegner,[1†] Robert R. Warner[15]

Ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, degradation of water quality, and anthropogenic climate change. Historical abundances of large consumer species were fantastically large in comparison with recent observations. Paleoecological, archaeological, and historical data show that time lags of decades to centuries occurred between the onset of overfishing and consequent changes in ecological communities, because unfished species of similar trophic level assumed the ecological roles of overfished species until they too were overfished or died of epidemic diseases related to overcrowding. Retrospective data not only help to clarify underlying causes and rates of ecological change, but they also demonstrate achievable goals for restoration and management of coastal ecosystems that could not even be contemplated based on the limited perspective of recent observations alone.

Few modern ecological studies take into account the former natural abundances of large marine vertebrates. There are dozens of places in the Caribbean named after large sea turtles whose adult populations now number in the tens of thousands rather than the tens of millions of a few centuries ago (*1*, *2*). Whales, manatees, dugongs, sea cows, monk seals, crocodiles, codfish, jewfish, swordfish, sharks, and rays are other large marine vertebrates that are now functionally or entirely extinct in most coastal ecosystems (*3*–*10*). Place names for oysters, pearls, and conches conjure up other ecological ghosts of marine invertebrates that were once so abundant as to pose hazards to navigation (*11*), but are witnessed now only by massive garbage heaps of empty shells.

Such ghosts represent a far more profound problem for ecological understanding and management than currently realized. Evidence from retrospective records strongly suggests that major structural and functional changes due to overfishing (*12*) occurred worldwide in coastal marine ecosystems over many centuries. Severe overfishing drives species to ecological extinction because overfished populations no longer interact significantly with other species in the community (*5*). Overfishing and ecological extinction predate and precondition modern ecological investigations and the collapse of marine ecosystems in recent times, raising the possibility that many more marine ecosystems may be vulnerable to collapse in the near future.

Importance of Historical Data

Most ecological research is based on local field studies lasting only a few years and conducted sometime after the 1950s without longer term historical perspective (*1*, *8*, *13*). Such observations fail to encompass the life-spans of many ecologically important species (*13*, *14*) and critically important environmental disturbances such as extreme cyclones or ENSO (El Niño–Southern Oscillation) events (*8*), as well as longer term cycles or shifts in oceanographic regimes and productivity (*15*–*17*). To help address this problem, we describe ecosystem structure predating modern ecological studies using well-dated time series based on biological (*18*, *19*), biogeochemical (*20*, *21*), physical (*22*), and historical (*23*) proxies that are informative over a variety of spatial scales and biogeographic realms (*24*). Although proxies vary in precision and clarity of the signals they measure, the use of multiple proxies that give the same ecological signal greatly increases confidence in results. Precision in age dating varies from centuries to a single year, season, or event in the exceptional case of varved sediments, ice cores, and written historical records (*25*). Precision decreases with the amount of biological or physical disturbance to the sediment analyzed (*26*).

We exploited data from many disciplines that span the period over which anthropogenic changes may have occurred. Because our hypothesis is that humans have been disturbing marine ecosystems since they first learned how to fish, our time periods need to begin well before the human occupation or European colonization of a coastal region. Broadly, our data fall into four categories and time periods:

1) Paleoecological records from marine sediments from about 125,000 years ago to the present, coinciding with the rise of modern *Homo sapiens*.

2) Archaeological records from human coastal settlements occupied after about 10,000 years before the present (yr B.P.) when worldwide sea level approached present levels. These document human exploitation of coastal resources for food and materials by past populations that range from small-scale aboriginal societies to towns, cities, and empires.

3) Historical records from documents, journals, and charts from the 15th century to the present that document the period from the first European trade-based colonial expansion and exploitation in the Americas and the South Pacific (*23*).

4) Ecological records from the scientific literature over the past century to the present covering the period of globalized exploitation of marine resources. These also help to calibrate the older records.

[1]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093–0244, USA. [2]Center for Tropical Paleoecology and Archeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama. [3]National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA. [4]Archie Carr Center for Sea Turtle Research and Department of Zoology, University of Florida, Gainesville, FL 32611, USA. [5]Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA. [6]Department of Anthropology, 155 Pettengill Hall, Bates College, Lewiston, ME 04240, USA. [7]Centre for Resource and Environmental Studies, Australian National University, Canberra, ACT 0200, Australia. [8]Department of Anthropology, University of Oregon, Eugene, OR 97403, USA. [9]U.S. Geological Survey, A-316 Earth and Marine Sciences Building, University of California, Santa Cruz, CA 95064, USA. [10]Center for Coral Reef Biodiversity, Department of Marine Biology, James Cook University, Townsville, QLD 4811, Australia. [11]Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, IL 60637, USA. [12]Institute of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell Street, Morehead City, NC 28557, USA. [13]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560–0121, USA. [14]School of Marine Sciences, University of Maine, Darling Marine Center, Orono, ME 04573, USA. [15]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA.

*To whom correspondence should be addressed. E-mail: jbcj@ucsd.edu

†Deceased.

Table 1. Retrospective records from coastal ecosystems that offer baselines that contrast with recent observations. Data source: P, paleoecologial; A, archaeological; H, historical; F, fisheries; E, ecological. Inferred causes: 1, fishing; 2, mechanical habitat destruction by fishing; 3, inputs. Abbreviations: BSi, biologically bound silica; DOP, degree of pyritization of iron; dec., decrease; inc., increase. References after *115* are located on *Science* Online (www.sciencemag.org/cgi/content/full/293/5530/629/DC1).

Parameter of interest	Location	Data source	Proxy	Time of baseline (yr B.P.)	Baseline observation or estimate	Recent observation or estimate	Trend	Inferred cause	Ref.
Kelp forests									
Sea Otter	Pacific Ocean	H, E	Area estimates	260	>100,000 individuals	30,000 individuals	>3.3-fold dec.	1	*116*
Stellar's sea cow	Alaska	H	Herd size	259	<5,000 sea cows	0	Extinction	1	*117*
Atlantic cod	Gulf of Maine	A	Cod vertebrae	3550	Mean body length of 1.0 m	Mean body length of 0.3 m	3-fold dec.	1	*113*
White abalone	California	E	Number per area	30	>2,000 per ha	1.0 ± 0.4 per ha	>2,000-fold dec.	1	*118*
Coral reefs									
Coral	Caribbean Sea	P, E	% sites with *A. palmata* dominant	125,000	80% of Pleistocene sites	15% of post-1982 sites	5.3-fold dec.	1	*114*
Coral	Caribbean Sea	P, E	% sites with *A. cervicornis* dominant	125,000	63% of Pleistocene sites	0% of post-1982 sites	100% loss	1	*114*
Coral	Bahamas	P, E	Standardized abundance of *A. cervicornis*	125,000	12	1	12-fold dec.	1	*119*
Coral	Belize	P	Relative abundance	3,130	*A. cervicornis* dominant	*A. cervicornis* absent	100% loss	1	*45*
Coral	Netherlands Antilles	E	Coral cover at 10 m	27	54% coral cover	31% coral cover	1.7-fold dec.	1	*120*
Coral	Jamaica	E	Coral cover at 10 m	23	73% coral cover	4% coral cover	18-fold dec.	1	*42*
Monk seal	Caribbean Sea	H	Historical reports	>300	Abundant	0	Extinction	1	*4, 68*
Coral	Moreton Bay	P, E	*Acropora* dominance in fossil reefs	8,000	Dominated reefs throughout Bay	Only one small *Acropora* reef left	Decrease	3	*121*
Tropical and subtropical seagrass beds									
Green turtle	Caribbean Sea	E	Biomass estimates	>300	>16.1 × 10^6 50-kg turtles	>1.1 × 10^6 50-kg turtles	15-fold dec.	1	*2, 122*
Green turtle	Caribbean Sea	H	Hunting, biomass estimates	>300	>3.3 × 10^7 adult turtles	>1.1 × 10^6 50-kg turtles	30-fold dec.	1	*1, 122*
Seagrass beds	Tampa Bay	H	Area	121	30,970 ha	10,759 ha	3-fold dec.	1, 2, 3	*123, 124*
Dugong	Eastern Australia	H	Herd size	>100	>1.0 × 10^6 estimated dugongs	14,000 estimated dugongs	>74-fold dec.	1	*125, 126*
Dugong	Moreton Bay	H	Herd size	107	>104,000 estimated dugongs	500 estimated dugongs	>208-fold dec.	1	*125, 127*
Oysters and eutrophication in estuaries									
Inputs	Chesapeake Bay	P	Sedimentation rate	1,900	0.04 cm $year^{-1}$	0.2 cm $year^{-1}$	5-fold inc.	3	*77*
Eutrophication	Chesapeake Bay	P	Total organic carbon	1,900	0.26 mg cm^{-2} $year^{-1}$	2.3 mg cm^{-2} $year^{-1}$	9-fold inc.	2, 3	*77*
Eutrophication	Chesapeake Bay	P	Centric/pennate diatom ratio	1,450	1:1 ratio	8:1 ratio	8-fold inc.	2, 3	*77*
Eutrophication	Chesapeake Bay	P	Dinoflagellate cysts (*Spiniferites* spp.)	>300	50% relative abundance	80% relative abundance	1.6-fold inc.	2, 3	*128*
Seagrass beds	Fleets Bay, CB	H	Area	63	273 ha	16 ha	17-fold dec.	1, 2, 3	*78*
Oyster reefs	Chesapeake Bay	F	Oyster landings	116	6.2 × 10^5 metric tons $year^{-1}$*	0.12 × 10^5 metric tons $year^{-1}$	52-fold dec.	2	*80*
Oyster reefs	Tangier Sound, CB	F	Area	122	44.6 km^2	0	100% loss	2	*129*
Anoxia	Cheapeake Bay	P	Degree of pyritization	1,900	0.32 DOP	0.51 DOP	2-fold inc.	2, 3	*77*
Seagrass beds	Botany Bay	H	Area of *Posidonia* beds	58	445 ha	188 ha	2.4-fold dec.	1, 2, 3	*130*
Eutrophication	Baltic Sea	P	Planktic diatom relative abundance	250	25% of total diatom abundance	80% of total diatom abundance	3-fold inc.	3	*131*
Eutrophication	Baltic Sea	P	Total organic carbon accumulation rate	138	3.2 gC m^{-2} $year^{-1}$	70 g C m^{-2} $year^{-1}$	22-fold inc.	3	*132*
Anoxia	Baltic Sea	P	Laminated sediments	100	5% of cores laminated	90% of cores laminated	18-fold inc.	3	*85*
Offshore benthic communities									
Oyster reefs	Foveaux Strait, NZ	F	Oyster landings	34	127 × 10^6 oysters/year*	15 × 10^6 oysters $year^{-1}$	8-fold dec.	2	*93*
Oyster reefs	Foveaux Strait, NZ	F	Reef by-catch per station	38	1 in 4 stations had reef by-catch	1 in 7 stations had reef by-catch	2-fold dec.	2	*93*
Eutrophication	Gulf of Mexico	P	Biologically bound silica	295	0.29% BSi	1.00% BSi	3.4-fold inc.	3	*106*
Eutrophication	Gulf of Mexico	P	Total organic carbon accumulation rate	100	2.4 mg C cm^{-2} $year^{-1}$	7.8 mg C cm^{-2} $year^{-1}$	3.3-fold inc.	3	*133*
Hypoxia	Gulf of Mexico	P	Benthic foraminifera	295	71 *Ammonia–Elphidium* Index	85 *Ammonia–Elphidium* Index	1.2-fold inc.	3	*134*
Eutrophication	Adriatic Sea	P	Eutrophic benthic foraminifera *Nonionella turgida*	170	6% relative abundance	38% relative abundance	6-fold inc.	3	*135*
Eutrophication	Adriatic Sea	P	Coccolithophorids	286	100 cells/g of sediment	1.6 × 10^6 cells/g of sediment	15,700-fold inc.	3	*136*

*Baseline taken from peak in landings.

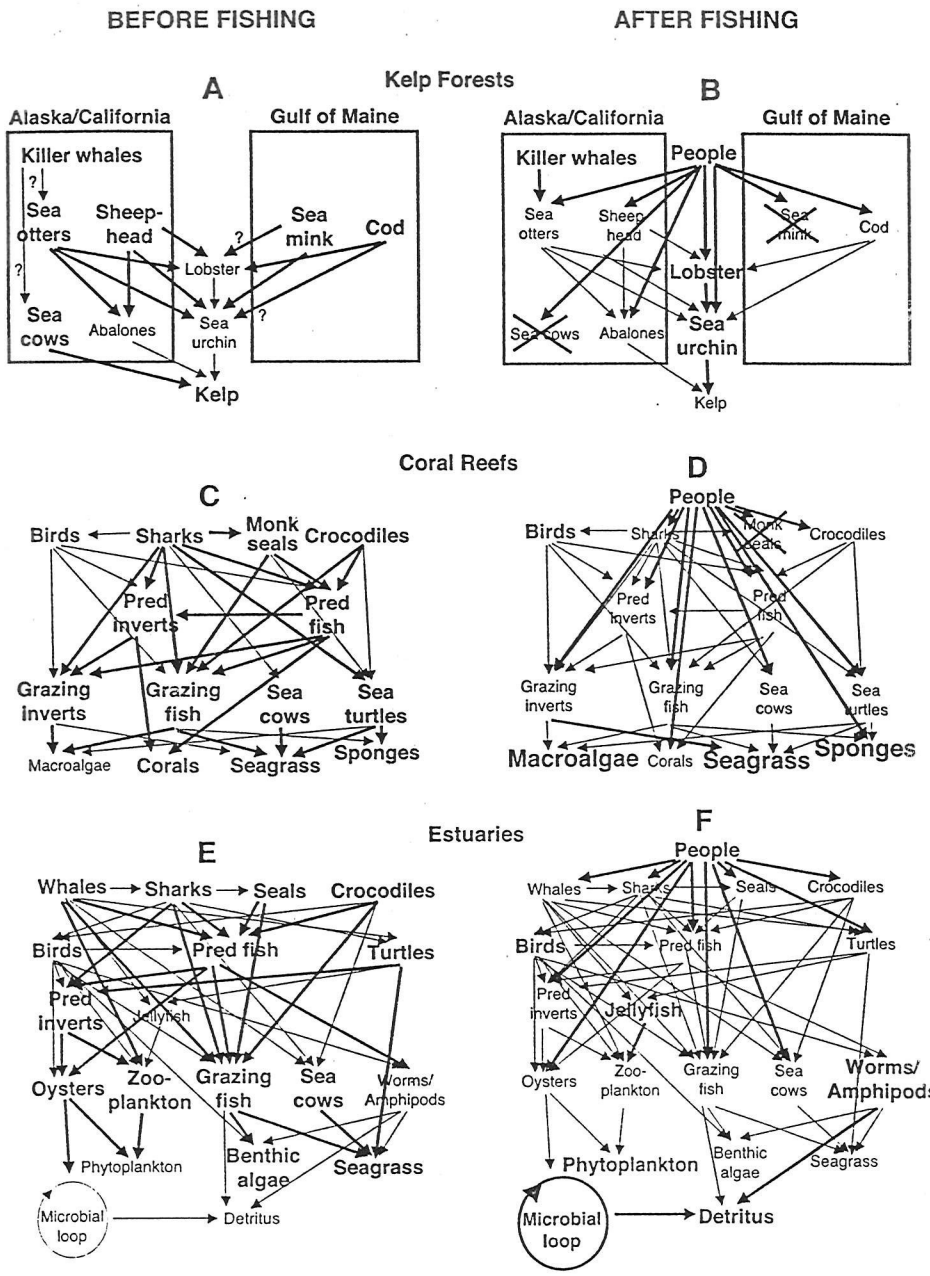


Fig. 1. Simplified coastal food webs showing changes in some of the important top-down interactions due to overfishing; before (left side) and after (right side) fishing. (A and B) Kelp forests for Alaska and southern California (left box), and Gulf of Maine (right box). (C and D) Tropical coral reefs and seagrass meadows. (E and F) Temperate estuaries. The representation of food webs after fishing is necessarily more arbitrary than those before fishing because of rapidly changing recent events. For example, sea urchins are once again rare in the Gulf of Maine, as they were before the overfishing of cod, due to the recent fishing of sea urchins that has also permitted the recovery of kelp. Bold font represents abundant; normal font represents rare; "crossed-out" represents extinct. Thick arrows represent strong interactions; thin arrows represent weak interactions.

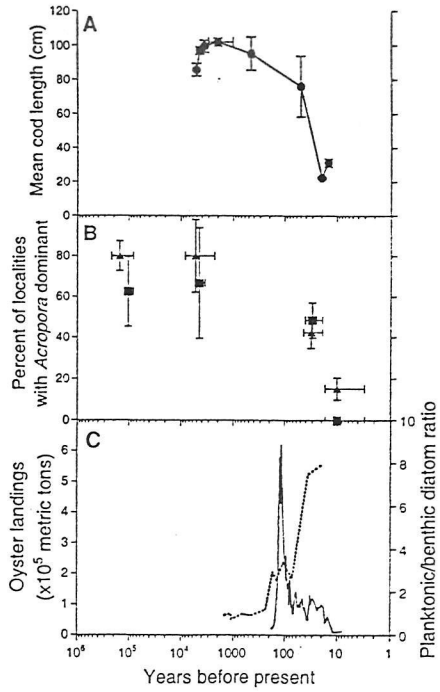


Fig. 2. Retrospective data showing baselines before ecosystem collapse. (A) Time series of mean body length of Atlantic cod from kelp forests in the coastal Gulf of Maine. The earlier five data points are derived from archaeological records, whereas the last three points are from fisheries data (*113*). Vertical bars represent the standard error. Horizontal bars represent the time range of data for a single interval of observations. (B) Paleoecological and ecological data showing the percentage of Caribbean localities with *Acropora palmata* (▲) or *A. cervicornis* (■) as the dominant shallow-water coral in the Late Pleistocene, Holocene, before 1983, and after 1983 (*114*). Percentages of localities are significantly different over the four time periods for *A. palmata* ($\chi^2 = 34.0$, $P < 0.0001$, df = 3) and *A. cervicornis* ($\chi^2 = 22.4$, $P < 0.0001$, df = 3). Vertical and horizontal bars are as in (A). (C) Paleoecological and fisheries data from Chesapeake Bay showing the ratio in abundance of planktonic to benthic diatoms (dotted line) (*77*) and landings of the oyster *Crassostrea virginica* (solid line) (*80*). The planktonic to benthic diatom ratio is a proxy for eutrophication that shows the relative amount of planktonic to benthic primary production (*77*). For over 1200 years this ratio remained fairly constant at about 1:1, but then increased threefold coincidentally with increased runoff of sediments and nutrients due to European agriculture after 1750. The ratio remained at about 3:1 between 1830 and 1930, after which it increased dramatically to about 8:1. Oyster landings show an initial increase in the early 19th century, peak in 1884, and subsequent collapse as deep channel reefs were destroyed by mechanical dredging (*80*). These data strongly imply that oysters were able to limit the potential for eutrophication induced by increased inputs of nutrients between 1750 and 1930 until oyster populations collapsed as a result of overfishing.

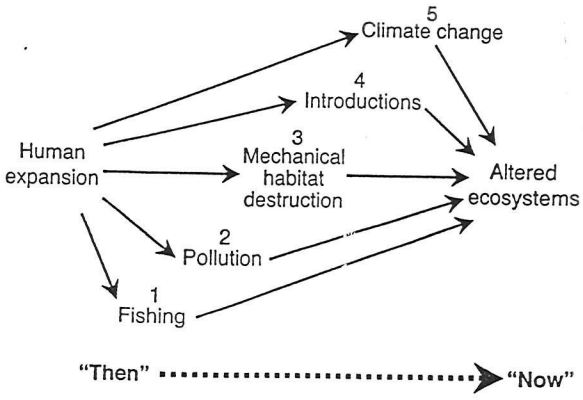


Fig. 3. Historical sequence of human disturbances affecting coastal ecosystems. Fishing (step 1) always preceded other human disturbance in all cases examined. This is the basis for our hypothesis of the primacy of overfishing in the deterioration of coastal ecosystems worldwide. Subsequent steps 2 through 5 have not been observed in every example and may vary in order.

Vol. 360: 63–72, 2008
doi: 10.3354/meps07526

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 22

OPEN ACCESS

Recovering a lost baseline: missing kelp forests from a metropolitan coast

Sean D. Connell[1,*], Bayden D. Russell[1], David J. Turner[2], Scoresby A. Shepherd[3], Timothy Kildea[4], David Miller[5], Laura Airoldi[6], Anthony Cheshire[7]

[1]Southern Seas Ecology Laboratories DX 650 418, School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia

[2]Regional Conservation, Department for Environment and Heritage, GPO Box 1047, Adelaide, South Australia 5001, Australia

[3]South Australian Research and Development Institute (Aquatic Sciences), PO Box 120, Henley Beach, South Australia 5022, Australia

[4]Australian Water Quality Centre, PMB 3, Salisbury, South Australia 5108, Australia

[5]Coast & Marine Conservation Branch, Natural and Cultural Heritage Directorate, Dept of Environment and Heritage, Keswick, South Australia 5035, Australia

[6]Università di Bologna, Via S. Alberto 163, 48100 Ravenna, Italy

[7]Science to Manage Uncertainty, 24 Winding Way, Belair, South Australia 5052, Australia

ABSTRACT: There is concern about historical and continuing loss of canopy-forming algae across the world's temperate coastline. In South Australia, the sparse cover of canopy-forming algae on the Adelaide metropolitan coast has been of public concern with continuous years of anecdotal evidence culminating in 2 competing views. One view considers that current patterns existed before the onset of urbanisation, whereas the alternate view is that they developed after urbanisation. We tested hypotheses to distinguish between these 2 models, each centred on the reconstruction of historical covers of canopies on the metropolitan coast. Historically, the metropolitan sites were indistinguishable from contemporary populations of reference sites across 70 km (i.e. Gulf St. Vincent), and could also represent a random subset of exposed coastal sites across 2100 km of the greater biogeographic province. Thus there was nothing 'special' about the metropolitan sites historically, but today they stand out because they have sparser covers of canopies compared to equivalent locations and times in the gulf and the greater province. This is evidence of wholesale loss of canopy-forming algae (up to 70%) on parts of the Adelaide metropolitan coast since major urbanisation. These findings not only set a research agenda based on the magnitude of loss, but they also bring into question the logic that smaller metropolitan populations of humans create impacts that are trivial relative to that of larger metropolitan centres. Instead, we highlight a need to recognise the ecological context that makes some coastal systems more vulnerable or resistant to increasing human-domination of the world's coastlines. We discuss challenges to this kind of research that receive little ecological discussion, particularly better leadership and administration, recognising that the systems we study out-live the life spans of individual research groups and operate on spatial scales that exceed the capacity of single research providers.

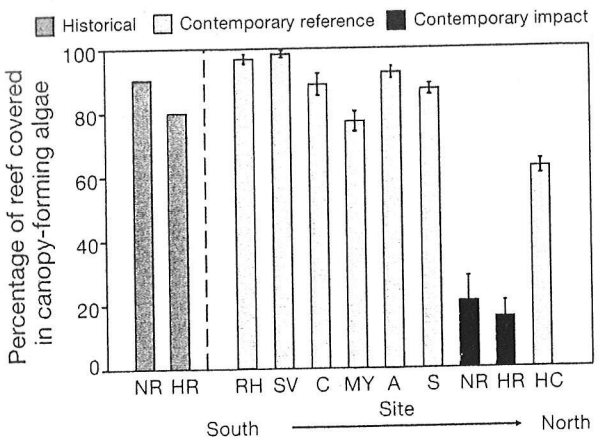


Fig. 2. Historical and contemporary cover of canopy-forming algae (mean ± SE of percentage cover) on impacted and reference rocky reefs in Gulf St. Vincent, South Australia. No error bars are presented for the historical covers that are single estimates. NR: Noarlunga Reef, HR: Horseshoe Reef, RH: Rapid Head, SV: Second Valley, C: Carrackalinga, MY: Myponga, A: Aldinga, S: Seaford, HC: Hallett Cove

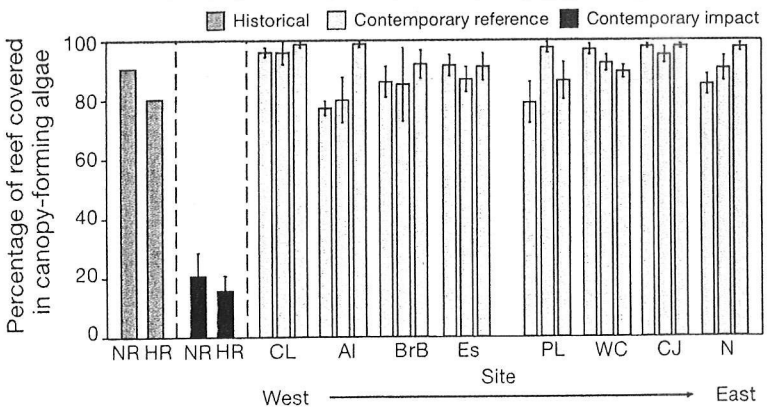


Fig. 4. Comparison of the historical and contemporary covers of canopy-forming algae (mean ± SE) on impacted and reference rocky sites across Western Australia and South Australia. Data are presented for 3 sites within each locality. NR: Noarlunga Reef, HR: Horseshoe Reef, RH: Rapid Head, CL: Cape Leeuwin, Al: Albany, BrB: Bremer Bay, Es: Esperance, PL: Port Lincoln, WC: West Cape, CJ: Cape Jervis, N: Newland Head. No error bars are presented for the historical covers that are single estimates

In conclusion, forecasted changes to abiotic environments at local and global scales (Harley et al. 2006) may be compounded by historical changes that have gone unnoticed. There has, therefore, never been a more pressing need for longer-term datasets to interpret the influence of human activities. The predominance of research focusing on local spatial scales over short time scales appears particularly counterproductive to our ability to detect change. While acquiring data for this research, we also identified that some of the greatest challenges to longer-term datasets may not be scientific. The storage and retrieval of data has become increasingly more problematic as rapid improvements in technology (e.g. computer software and hardware) chain current archival efforts to antiquated technology. Already, some 'modern' technology has become redundant, so that stored information is impossible to retrieve (e.g. tape drives and specific kinds of image projectors that no longer exist). Perhaps clay tablets that record human history represent some of our longest lasting archival media (albeit of low storage capacity) that capture change on time-scales we are becoming more aware of and increasingly concerned about (e.g. climate change).

Finally, we emphasise the lack of coherent research across time, matched by discordant research across space and taxonomic scales, and a need for a broader vision by those charged with the administration of science (i.e. its accountability and fundability). Indeed, never has there been a greater need for better leadership of the ecological sciences. The discipline of ecology needs leadership that encourages rather than penalises collaboration and inheritance of data. Our life spans are often less than the duration of the organisms we study, and our expertise and capacity to research multiple localities and levels of biological organisation are limited. We are not naïve in understanding that institutional reform is difficult and slow, and good leaders occur infrequently across generations; hence, we encourage some of this progress to fall on the shoulders of individuals with an ability to focus on collective rather than personal goals, and on long-term progress. Indeed, many of the environmental changes we only now recognise were set in motion long ago.

Journal of the Marine Biological Association of the United Kingdom, page 1 of 10. © Marine Biological Association of the United Kingdom, 2011
doi:10.1017/S0025315411001317

The regional recovery of *Nucella lapillus* populations from marine pollution, facilitated by man-made structures

SIMON BRAY[1], EMILY C. MCVEAN[1], ANDREW NELSON[2], ROGER J.H. HERBERT[3], STEPHEN J HAWKINS[4] AND MALCOLM D. HUDSON[1]

[1]Faculty of Engineering and Environment, University of Southampton, Highfield, Southampton, Hampshire, SO17 1BJ, [2]Field Studies Council, Nettlecombe Court, The Leonard Wills Field Centre, Williton, Taunton, Somerset, TA4 4HT, [3]School of Conservation Sciences, Christchurch House, Bournemouth University Fern Barrow Talbot, Campus, Poole, Dorset, BH12 5BB, [4]Faculty of Natural and Environmental Sciences, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ, UK

The dogwhelk Nucella lapillus *experienced localized extinction in the 1980s and 1990s due to the use of tributyltin (TBT) antifoulants, causing imposex in females. The aim of this study was to establish the extent of the return of the species across the mainland coast of central southern England as TBT use has been progressively restricted, and to quantify the extent of imposex impact on the populations present. We surveyed from Poole to Selsey where isolated populations had become extinct, and the Isle of Wight where some populations had persisted. We found evidence that since TBT restrictions, recolonization and colonization by* N. lapillus *has been rapid. By 2007–2008, of the eleven surveyed mainland sites, seven were colonized, although indications of reduced imposex impacts were mixed. Distribution had also extended on the Isle of Wight and populations were larger with less imposex impact in sites with long term populations. The lack of continuous suitable habitat blocks and the hydrodynamic complexity of the region, leads us to hypothesize that recovery has been facilitated by man-made structures which may be acting as 'stepping stones'. Populations that have become established on engineered structures such as sea walls, breakwaters and rock groynes demonstrate accelerated recovery in the region as TBT in the environment has generally declined. Sites with suitable substrates and food sources near to ports were either not recolonized or had small populations with imposex evident. For species with a short pelagic larval stage or with direct development, population connectivity between patches of harder substrata along hydrodynamically complex coastlines may be greater than previously thought.*

Table 2. Site characteristics, dogwhelk population and imposex data for Isle of Wight for 1997 and 2007. Abundance data show number found in 30 minutes.

Site	Substrate	Abundance 1997	Abundance 2007	% females showing imposex 1997	% females showing imposex 2007	RPSI 1997 %	RPSI 2007 %	Median VDS 1997	VDS range 1997	Median VDS 2007	VDS range 2007
Bembridge	Rocky shore, reefs and boulders	117	338	100	80	11	0.420	3	1–4	0	0–4
Ventnor	Rocky shore, rocky boulders	69	242	N/A	86	N/A	0.070	N/A	N/A	0	0
Hanover Point	Rocky shore, reefs and boulders	208	372	100	81	18.2	0.096	3	2–4	0	0–4
Yarmouth	Pier piles	0	278	N/A	55	N/A	0.004	N/A	N/A	0	0–2
Cowes	Groyne	3	73	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

RSPI, relative penis size index; VDS, vas deferens sequence; N/A, not applicable.

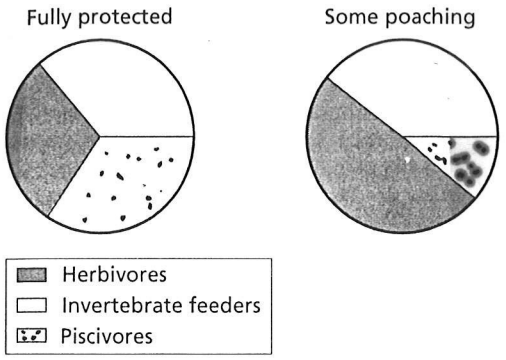


Fig. 12.11 Trophic structure (by biomass) of fish communities in Seychelles marine reserves that are either fully protected, or subject to a small amount of fishing and poaching. After Jennings and Kaiser (1998).

Effects of Marine Reserves on Adjacent Fisheries

Callum M. Roberts,[1,2]* James A. Bohnsack,[3] Fiona Gell,[2] Julie P. Hawkins,[2] Renata Goodridge[4]

Marine reserves have been widely promoted as conservation and fishery management tools. There are robust demonstrations of conservation benefits, but fishery benefits remain controversial. We show that marine reserves in Florida (United States) and St. Lucia have enhanced adjacent fisheries. Within 5 years of creation, a network of five small reserves in St. Lucia increased adjacent catches of artisanal fishers by between 46 and 90%, depending on the type of gear the fishers used. In Florida, reserve zones in the Merritt Island National Wildlife Refuge have supplied increasing numbers of world record–sized fish to adjacent recreational fisheries since the 1970s. Our study confirms theoretical predictions that marine reserves can play a key role in supporting fisheries.

Marine reserves, areas that are closed to all fishing, have been attracting much attention for their dual potential as conservation and fishery management tools (*1–5*). A synthesis of more than 100 studies of reserves worldwide shows that protection from fishing leads to rapid increases in biomass, abundance, and average size of exploited organisms and to increased species diversity (*6*). Such effects are of great interest to fishery managers, because rebuilding

MARINE ECOLOGY PROGRESS SERIES

Inter-Research
Marine Ecology Progress Series

MEPS 264:15-20 (2003)

Abstract

Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines

Garry R. Russ[1,*], Angel C. Alcala[2], Aileen P. Maypa[2]

[1]School of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland 4811, Australia
[2]Silliman University Angelo King Center for Research and Environmental Management, Silliman University, Dumaguete City 6200, Philippines

*Email: garry.russ@jcu.edu.au

ABSTRACT: The use of no-take marine reserves as fisheries management tools is controversial. A major expectation of marine reserves is that they will become net exporters of adult biomass (the 'spillover effect'). Herein, we show that the biomass of the surgeonfish *Naso vlamingii* tripled over 18 yr (1983 to 2001) in a reserve at Apo Island, Philippines. Over time, the biomass of *N. vlamingii* increased by a factor of 40 outside but close to the reserve boundaries (200 to 250 m) but not at greater distances (250 to 500 m). In 2000/2001 hook-and-line catch per unit effort (CPUE) for *N. vlamingii* was 45 times higher within 200 m of the reserve boundary than for all other fishing grounds combined, with 62.5% of the hook-and-line catch records being recorded within 200 m either side of the reserve, in just 11% of the reef fishing area. This comprises some of the best evidence that reserves can benefit fisheries by spillover.

Ecology Letters, (2002) 5: 361–366

REPORT

Marine reserves have rapid and lasting effects

Benjamin S. Halpern*
and Robert R. Warner
Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, 93106, U.S.A.
**Correspondence:*
E-mail: halpern@lifesci.ucsb.edu

Abstract

Marine reserves are becoming a popular tool for marine conservation and resource management worldwide. In the past, reserves have been created with little understanding of how they actually affect the areas they are intended to protect. A few recent reviews have evaluated how reserves in general affect the density and biomass of organisms within them, but little work has been done to assess temporal patterns of these impacts. Here we review 112 independent measurements of 80 reserves to show that the higher average values of density, biomass, average organism size, and diversity inside reserves (relative to controls) reach mean levels within a short (1–3 y) period of time and that the values are subsequently consistent across reserves of all ages (up to 40 y). Therefore, biological responses inside marine reserves appear to develop quickly and last through time. This result should facilitate their use in the management of marine resources.

Keywords

Marine conservation, marine protected areas, marine reserves, temporal effects.

Ecology Letters (2002) 5: 361–366

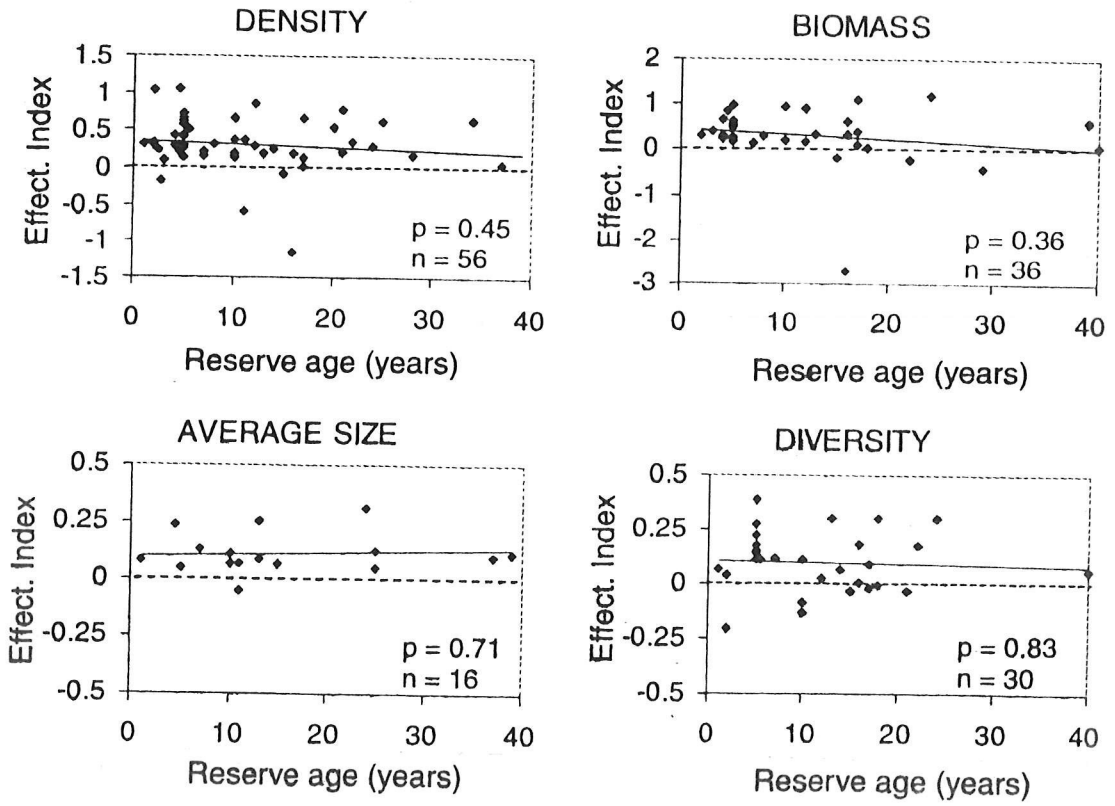


Figure 1 Log_{10} ratios of values from inside a reserve vs. values from a reference site for density (no./area), biomass (kg/area), average organism size, and diversity (species richness) as a function of the age of the reserve. For the majority of cases, these data represent comparisons between values inside vs. outside the reserve. Data are plotted as the log_{10} of the ratio (effectiveness index) vs. reserve age at the time measurements were made. Because ratios are log_{10}-transformed, at effectiveness index = 0 reserves did not differ from their reference site. Points above this line represent reserves in which the value of the biological measure was higher inside the reserve; points below the line represent reserves in which these values were lower. In all cases slopes of regression lines are not significantly different from zero (sample size and *P*-values for linear regression analyses for each biological measure are in the lower right corner of each plot), whereas grand mean values were all greater than zero (Student's *t*-test, $P < 0.025$ for all cases).

Mar Biol (2007) 151:1153–1161
DOI 10.1007/s00227-006-0557-0

RESEARCH ARTICLE

Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data

C. Ojeda-Martinez · J. T. Bayle-Sempere · P. Sánchez-Jerez · A. Forcada · C. Valle

Abstract Marine protected areas (MPA) produce a positive effect on fish populations, but this may be difficult to identify due to the high temporal variability of populations. Meta-analysis is an option for analysing data from different sources and sampling designs and it can address problems related to temporal and spatial variability in fish populations. We analysed fish abundance data from visual counts conducted in summer, from 1996 to 2002, in the MPA of Tabarca (Alicante, Spain). The results showed an overall positive effect of protection at the species and family levels. Overall abundance of fishes inside the reserve was, on average, 1.22 times higher than outside the reserve boundaries. Positive effect of protection was found for *Boops boops*, *Diplodus annularis*, *Diplodus cervinus*, *Epinephelus marginatus*, *Epinephelus costae* and *Epinephelus aenus*. Species of Labrids were not affected by protection, except for *Thalassoma pavo* and *Symphodus ocellatus*. Meta-analysis of temporal data allows evaluation of the protection MPA provide and is particularly useful when data sources have different experimental designs or sampling programs. The Tabarca MPA has benefited fish populations by increasing their abundance and we suggest that meta-analysis is a complementary tool for the management of MPAs.

Table 2 Values of protection effect and significance for each family meta-analysed

Family	Effect
Belonidae	1.08^{ns}
Centracanthidae	1.94^{***}
Congridae	-0.80^{ns}
Haemulidae	1.26^{ns}
Labridae	0.69^{***}
Moronidae	2.54^{ns}
Mugilidae	0.08^{ns}
Mullidae	-3.12^{**}
Sciaenidae	4.18^{***}
Scorpaenidae	-0.17^{ns}
Serranidae	1.259^{**}
Sparidae	1.536^{***}

ns not significant
$^{**}P < 0.01$, $^{***}P < 0.001$

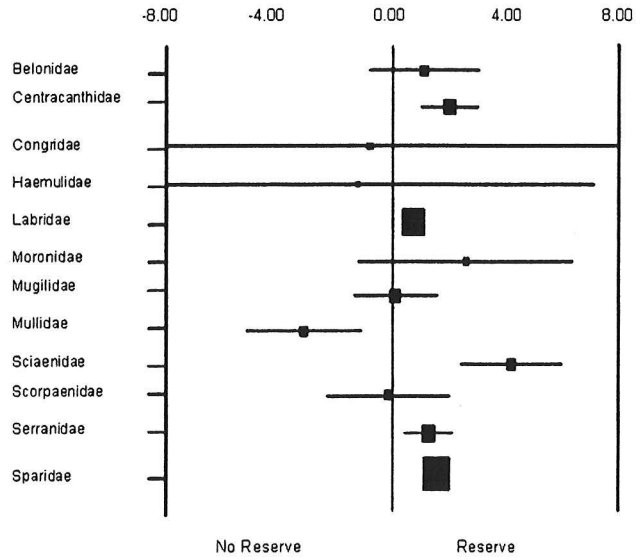


Fig. 3 Protection effect on different families. Reserve effect value and bootstrap-generated confidence intervals are shown. See Table 2 for further details

Vol. 351: 221–233, 2007
doi: 10.3354/meps07112

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 6

Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing

Alan M. Friedlander[1,*], Eric Brown[2,3], Mark E. Monaco[4]

[1]NOAA/NOS/NCCOS Center for Coastal Monitoring and Assessment, Biogeography Branch and the Oceanic Institute, 41-202 Kalanianaole Highway Waimanalo, Hawaii 96795, USA

[2]Hawaii Department of Land and Natural Resources, Division of Aquatic Resources, Wailuku, Hawaii 96793, USA

[3]National Park Service, Kalaupapa National Historical Park, Hawaii 96742, USA

[4]NOAA/NOS/NCCOS Center for Coastal Monitoring and Assessment, Biogeography Branch, 1305 East West Highway, Silver Spring, Maryland 20190, USA

ABSTRACT: Over the past 4 decades, Hawaii has developed a system of Marine Life Conservation Districts (MLCDs) to conserve and replenish marine resources. These MLCDs vary in size, habitat quality, and management regimes, providing an excellent opportunity to test hypotheses concerning marine protected area (MPA) design and function using multiple discreet sampling units. Digital benthic habitat maps for all MLCDs and adjacent habitats were used to evaluate the efficacy of existing MLCDs and adjacent habitats using a spatially explicit stratified random sampling design. Most fish assemblage characteristics (e.g. species richness, biomass, number of individuals) were highest in colonized hard bottom habitats (>10% live coral cover), followed by uncolonized hard bottom habitats (<10% live coral cover), macroalgae, and sand, respectively. Although biomass was low in sand habitats, apex predators accounted for 62% of the biomass on sand within MLCDs, highlighting the importance of this habitat in reserve design. Within habitats, values for assemblage characteristics were typically higher for MLCDs compared with adjacent areas, emphasizing the importance of protection from fishing irrespective of habitat. Rugosity explained much of the variability in species richness and biomass across all locations. Overall, MLCDs protected from fishing, with high habitat complexity and good habitat quality (e.g. high coral cover and low macroalgae cover), had higher values for most fish assemblage characteristics. Integrating mapping and assessment of reef fish habitat utilization patterns allowed for a robust approach to MPA evaluation and can help inform decisions about MPA design and effectiveness, as well as helping to define essential fish habitat and ecosystem function.

Marine Biology (2006) 148: 1213–1220
DOI 10.1007/s00227-005-0181-4

RESEARCH ARTICLE

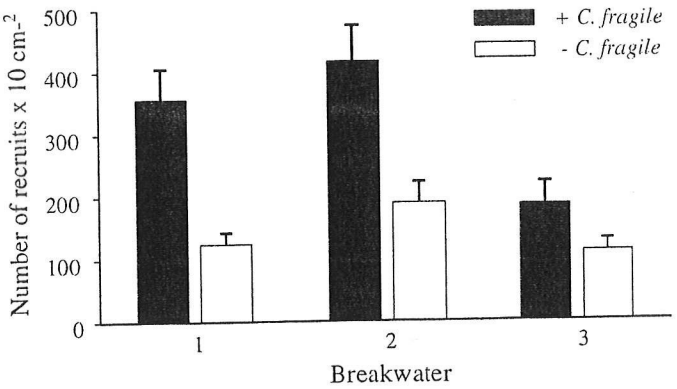
F. Bulleri · L. Airoldi · G.M. Branca · M. Abbiati

Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels

Received: 23 May 2005 / Accepted: 20 July 2005 / Published online: 29 November 2005
© Springer-Verlag 2005

Abstract The green macroalga, *Codium fragile* ssp. *tomentosoides*, is an important component of sheltered low-shore assemblages on breakwaters along sandy shores in the northern Adriatic Sea. Macroscopic thalli of *C. fragile* are not perennial, but develop from propagules and/or undifferentiated forms in early spring, when the dominant native space-occupier, the mussel *Mytilus galloprovincialis*, recruits. By mid-summer, rapid growth of *C. fragile* leads to the formation of a dense canopy. We investigated the effects of juvenile and adult thalli of *C. fragile* on recruitment, survival and growth of mussels. Two experiments tested the hypotheses: (1) that recruitment of mussels is greater within patches of juvenile thalli (primordia) of *C. fragile* than on adjacent bare surfaces; (2) that the presence of a canopy of *C. fragile* affects the survival and growth of mussel recruits. The number of recruits of mussels was significantly larger within clumps of primordia of *C. fragile* than on bare surfaces. The removal of the canopy of *C. fragile* affected negatively the density of mussels after 2 months from the start of the experiment, but there were no effects on the mean size of individuals, nor on the size–frequency distribution. The same trend persisted after 4 months from the start of the experiment. These results show that re-colonisation of space by mussels is enhanced by *C. fragile*. Given that mussels, in turn, have the potential to reduce recruitment rates of *C. fragile*, quick recovery of mussel beds after disturbances could be crucial for controlling the abundance of this alga on breakwaters. Results also suggest that the effects of introduced species on native assemblages can be explained only through studies encompassing different life-stages of interacting organisms.

Fig. 2 Mean number of recruits of mussels within patches with (+ *C. fragile*) and without (- *C. fragile*) primordia of *C. fragile* in March 2004, separately for each breakwater. Data are averages (± SE) from 16 replicate quadrats (4 quadrats on each of 4 blocks)



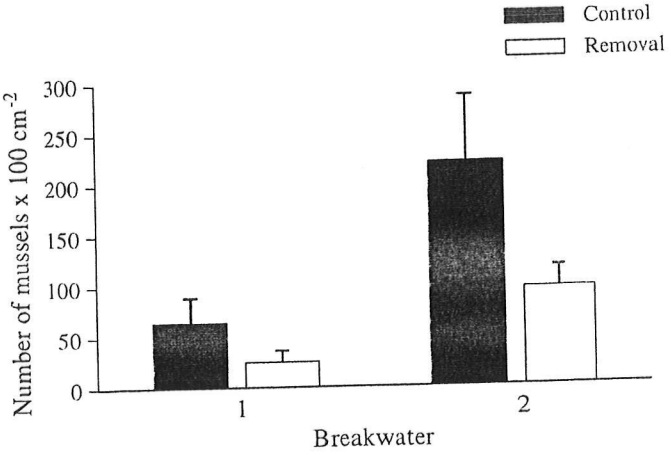


Fig. 3 Mean number of juvenile mussels in control and canopy removal blocks after 2 months from the start of the experiment, separately for each breakwater. Data are averages (± SE) from nine replicate quadrats (three quadrats on each of three blocks)

Collapse and Conservation of Shark Populations in the Northwest Atlantic

Julia K. Baum,* Ransom A. Myers, Daniel G. Kehler, Boris Worm, Shelton J. Harley, Penny A. Doherty

Overexploitation threatens the future of many large vertebrates. In the ocean, tunas and sea turtles are current conservation concerns because of this intense pressure. The status of most shark species, in contrast, remains uncertain. Using the largest data set in the Northwest Atlantic, we show rapid large declines in large coastal and oceanic shark populations. Scalloped hammerhead, white, and thresher sharks are each estimated to have declined by over 75% in the past 15 years. Closed-area models highlight priority areas for shark conservation, and the need to consider effort reallocation and site selection if marine reserves are to benefit multiple threatened species.

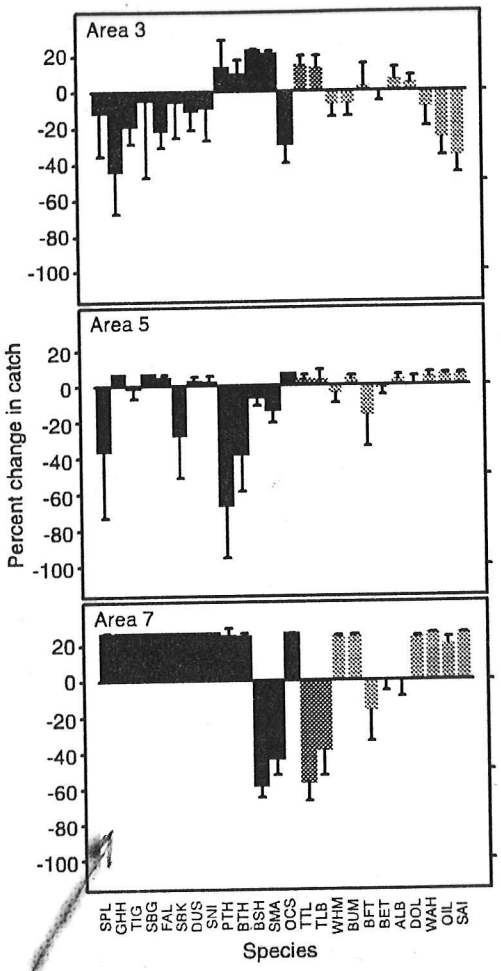


Fig. 4. Results from closed-area model showing predicted changes in catch as caused by year-round longline closure of Areas 3, 5, and 7. Remaining areas are shown in fig. S2. Results for the constant-quota (above and fig. S2) and constant-effort (fig. S3) scenarios were similar. Negative values refer to reductions in catch. Error bars are 95% bootstrap confidence intervals, accounting for the uncertainty in the observer estimates of species composition. Black bars represent sharks (SPL, scalloped hammerhead; GHH, great hammerhead; TIG, tiger; SBG, bignose; FAL, silky; SBK, blacktip; DUS, dusky; SNI, night; PTH, common thresher; BTH, bigeye thresher; BSH, blue; SMA, shortfin mako; OCS, oceanic whitetip), dark gray bars represent sea turtles (TTL, loggerhead; TLB, leatherback), and light gray bars represent finfish (WHM, white marlin; BUM, blue marlin; BFT, bluefin tuna; BET, bigeye tuna; ALB, albacore tuna; DOL, common dolphinfish; WAH, wahoo; OIL, oilfish; SAI, Atlantic sailfish). See table S2 for scientific names and conservation status.

Model results show that marine reserves can indirectly cause harm if fishing effort is merely displaced. For example, the closure of Area 7 meets its objective in reducing sea turtle bycatch and also protects sharks of lower conservation concern: blue and mako sharks. However, this closure increases catch of almost every other species (Fig. 4), because effort is redistributed to areas of higher species diversity.

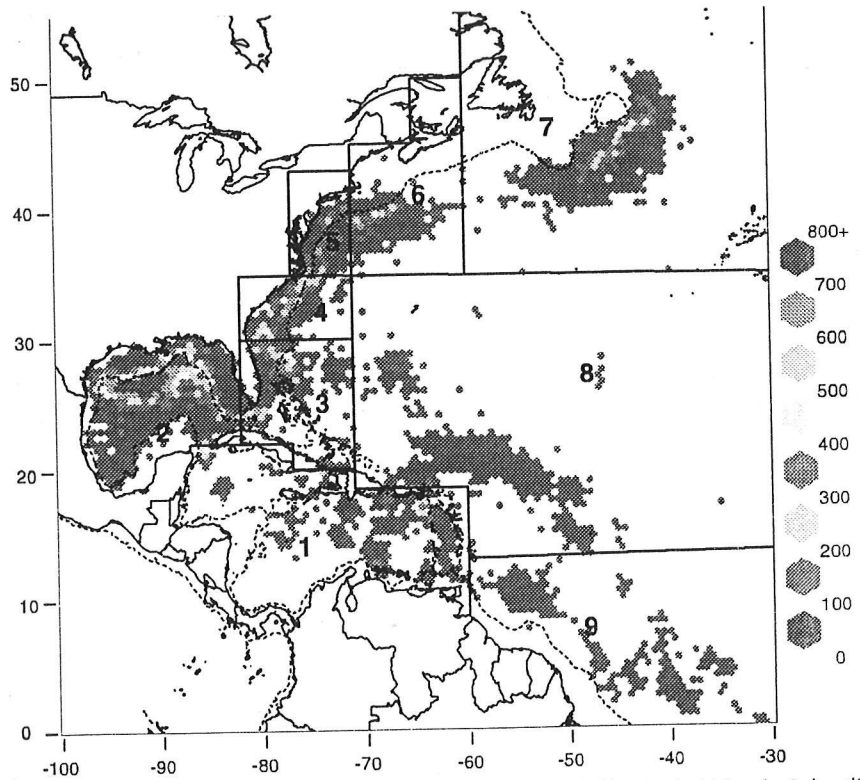


Fig. 1. Map of the Northwest Atlantic showing the distribution of effort in the U.S. pelagic longline fishery between 1986 and 2000, categorized by number of sets (0 to 800$^+$), within the nine areas assessed: 1, Caribbean; 2, Gulf of Mexico; 3, Florida East Coast; 4, South Atlantic Bight; 5, Mid Atlantic Bight; 6, Northeast Coastal; 7, Northeast Distant; 8, Sargasso/North Central Atlantic; 9, Tuna North/Tuna South. Areas were modified from the U.S. National Marine Fisheries Service classification for longline fisheries. The 1000-m coastal isobath (dotted line) is given for reference.

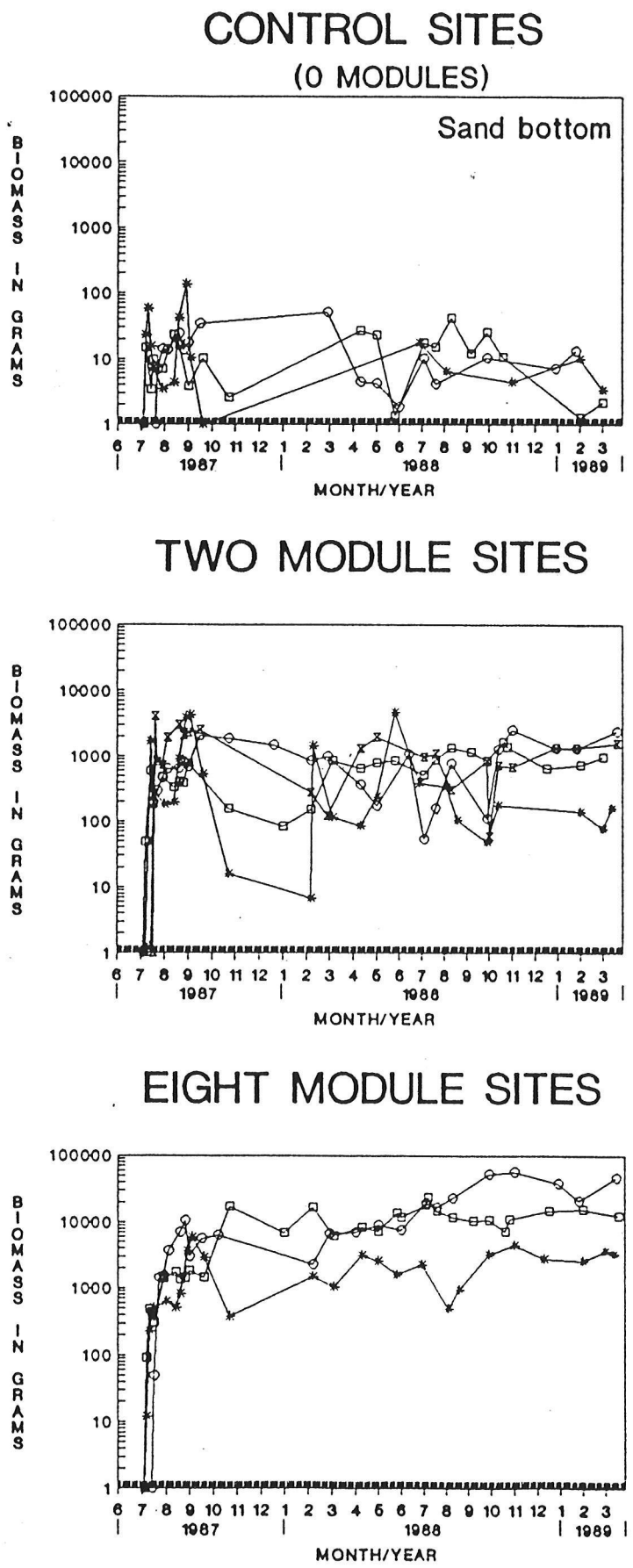


Figure 3.8 Colonization and seasonal variation in fish biomass, as a function of reef size, at artificial reefs deployed off Miami, Florida. (*Figure continues.*)

ELSEVIER

Journal of Experimental Marine Biology and Ecology 340 (2007) 25–39

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Differential recruitment of benthic communities on neighboring artificial and natural reefs

S. Perkol-Finkel *, Y. Benayahu

Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Tel Aviv, P.O.B. 39040, Israel

Received 10 June 2006; received in revised form 15 July 2006; accepted 8 August 2006

Abstract

Shedding light on the ability of benthic artificial reef (AR) communities to resemble those of a natural reef (NR) is of great importance if we are to harness ARs as tools for rehabilitation and restoration of degraded marine habitats. Studying recruitment processes to experimental settlement plates attached to ARs and NRs reveal the factors that shape community structure at the two reef types, and determine the ability of an AR to support communities similar to those found in adjacent natural habitats. In this study, conducted in Eilat (Red Sea), we used settlement plates to test the hypothesis that differences in benthic communities between ARs and NRs are derived from differential recruitment processes. A monitoring period of 18 months revealed great differences in the recruitment of corals and other benthic communities between the studied ARs and adjacent NRs. The ARs were either made of PVC or metal and 10–17 years old when the study commenced. The recruitment of soft corals reflected the species assemblage found in the area, consisting mainly of the family Nephtheidae and Xeniidae, species, while that of stony corals was mostly determined by the life history traits of the recruited taxa, e.g., the opportunistic nature of the family Pocilloporidae. Benthic organisms, mainly filter feeders like bryozoans, bivalves, sponges and tunicates, were more abundant at the ARs than at the NRs, mainly on the underside of the plates. We suggest that this differential recruitment resulted from a synergistic effect of abiotic and biotic factors, including current regime, sedimentation load and larval settlement preferences, which subsequently differentiated the composition of the benthic communities at the ARs and NRs. Thus, in order to construct an AR for restoration purposes, it must offer similar structural features to those found in the natural surrounding, leading to recruitment of local taxa. However, if the AR and NR will differ structurally, the composition of recruits will also differ and eventually the communities at the two reef types will become distinct, hereby increasing the species diversity in the area.

Table 4
Dissimilarity between the reef types at the Dolphin Reef and pyramid sites pooled over time, based on average abundance (square root transformed) of all community components

Community component	Dolphin AR	Dolphin NR	Average dissimilarity $\bar{\delta}=53.78$		
	Average abundance	Average abundance	Average dissimilarity	$\bar{\delta}_i\%$	$\sum\bar{\delta}_i\%$
Bare space	21.35	38.72	14.09	26.21	26.21
Bryozoans	19.88	2.64	11.39	21.18	47.39
Bivalves	6.02	5.38	6.92	12.86	60.25
Xenia/Heteroxenia sp.	2.67	1.94	4.62	8.59	68.84
Sponges	1.44	1.68	3.13	5.83	74.67
Stylophora/Pocillopora sp.	0.04	1.40	2.86	5.32	79.99
Serpulid worms	1.54	0.77	1.60	4.38	84.82
Tunicates-colonial	1.65	0.34	1.89	3.52	88.33
Coralline algae	1.63	1.70	1.58	2.94	91.27
Tunicates-solitary	0.48	0.09	1.29	2.39	93.66
Rhytisma fulvum fulvum	0.23	0.09	1.03	1.91	95.57
Dendronephthya hemprichi	0.33	0.00	0.89	1.66	97.24
Acabaria sinaica	0.08	0.02	0.37	0.68	97.92
Scleronephthya corymbosa	0.31	0.00	0.36	0.66	98.58
Soft corals (unidentified)	0.10	0.02	0.32	0.59	99.17
Stereonephthya cundabiluensis	0.04	0.00	0.15	0.28	99.44
Litophyton sp.	0.00	0.04	0.13	0.24	99.68
Paralemnalia thyrsoides	0.00	0.04	0.10	0.18	99.86
Cyphastrea chalcidicum	0.00	0.02	0.07	0.14	100.00

Community component	Pyramid AR	Pyramid NR	Average dissimilarity $\bar{\delta}=57.61$		
	Average abundance	Average abundance	Average dissimilarity	$\bar{\delta}_i\%$	$\sum\bar{\delta}_i\%$
Bare space	21.88	8.85	12.95	22.48	22.48
Bryozoans	18.33	11.42	10.87	18.88	41.35
Bivalves	10.25	14.75	9.35	16.23	57.58
Sponges	9.85	4.04	7.27	12.62	70.20
Xenia/Heteroxenia sp.	0.17	3.38	5.83	10.12	80.32
Tunicates-colonial	1.00	2.90	2.85	4.94	85.26
Serpulidae	1.35	1.08	2.30	3.99	89.25
Coralline algae	1.96	1.98	1.79	3.12	92.37
Tunicates-solitary	0.63	0.06	1.29	2.25	94.61
Rhytisma fulvum fulvum	0.25	0.13	0.96	1.66	96.27
Cyphastrea chalcidicum	0.04	0.10	0.47	0.82	97.09
Echinophyllia sp.	0.04	0.02	0.30	0.52	97.62
Stylophora/Pocillopora sp.	0.04	0.04	0.29	0.50	98.12
Stony corals (unidentified)	0.00	0.08	0.20	0.35	98.46
Dendronephthya hemprichi	0.02	0.02	0.18	0.32	98.78
Favia sp.	0.02	0.02	0.16	0.29	99.07
Galaxea fascicularis	0.00	0.04	0.15	0.26	99.33
Soft corals (unidentified)	0.00	0.04	0.13	0.23	99.56
Turbinaria sp.	0.02	0.00	0.10	0.18	99.74
Porites sp.	0.02	0.00	0.09	0.15	99.89
Acabaria sinaica	0.00	0.02	0.07	0.11	100.00

$\bar{\delta}_i\%$=percent contribution of ith component to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the reef types.
$\sum\bar{\delta}_i\%$=cumulative percentage.
Community components are listed in decreasing order of importance in contribution to $\bar{\delta}$.
Artificial reef=AR, natural reef=NR.

Mar Biol (2007) 151:887–895
DOI 10.1007/s00227-006-0552-5

RESEARCH ARTICLE

Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions?

Tim M. Glasby · Sean D. Connell · Michael G. Holloway · Chad L. Hewitt

Abstract We identified different distributions of marine nonindigenous species (NIS) and native species on some artificial structures versus natural reefs and using experimental manipulations, revealed some possible causal mechanisms. In well-established subtidal assemblages, numbers of NIS were 1.5–2.5 times greater on pontoons or pilings than on rocky reefs, despite the local species pool of natives being up to 2.5 times greater than that of NIS. Conversely, on reefs and seawalls, numbers of native species were up to three times greater than numbers of NIS. Differential recruitment to different positions and types of surfaces appeared to influence distribution patterns. NIS recruited well to most surfaces, particularly concrete surfaces near the surface of the water, whilst natives occurred infrequently on wooden surfaces. The position of rocky reefs and seawalls close to the shore and to the seabed appeared to make them favourable for the recruitment of natives, but this positioning alone does not hinder the recruitment of NIS. We argue that pontoons and pilings represent beachheads (i.e. entry points for invasion) for many nonindigenous epibiota and so enhance the spread and establishment of NIS in estuaries. Habitat creation in estuaries may, therefore, be a serious threat to native biodiversity.

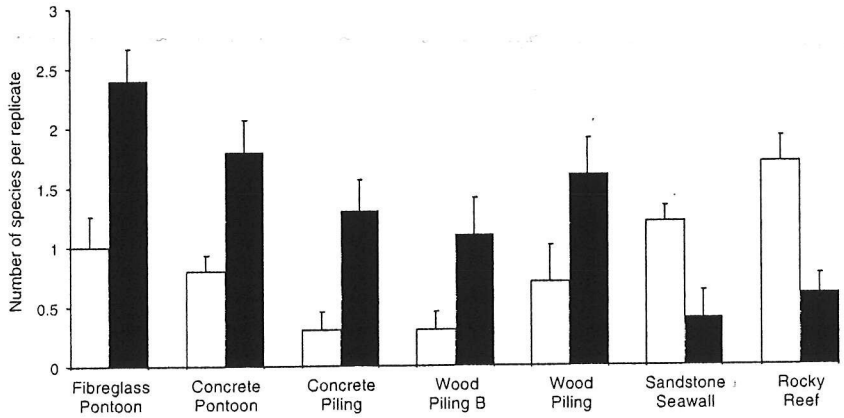


Fig. 1 Mean (±SE) number of native species (*white*) and NIS (*black*) per replicate in established assemblages on artificial structures and on natural sandstone rocky reefs. Artificial structures are: fibreglass pontoons, concrete pontoons, concrete pilings, wooden pilings with bark, wooden pilings stripped of bark, sandstone brick seawalls. Data from five replicates at each of two sites have been pooled

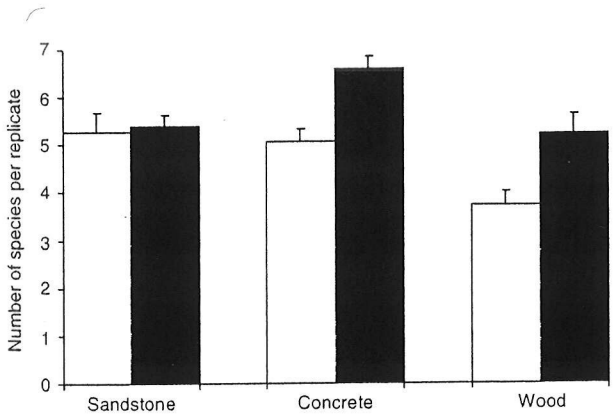


Fig. 4 Mean number (±SE) of native species (*white*) and NIS (*black*) that recruited to sandstone, concrete or wooden settlement panels deployed subtidally on rocky reefs for 30 weeks. Data from three sites were not significantly different and have been combined here

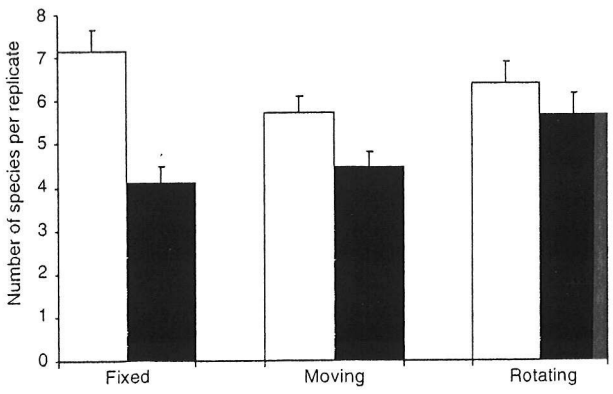


Fig. 5 Mean number (±SE) of native species (*white*) and NIS (*black*) sampled on sandstone settlement panels that did not move (*fixed*), moved up and down (*moving*) or rotated and orientated parallel to currents (*rotating*). Panels were deployed twice for 29 weeks at two sites and times and sites have been combined in this graph

POLICY FORUM: ECOLOGY

Direct Payments to Conserve Biodiversity

Paul J. Ferraro and Agnes Kiss

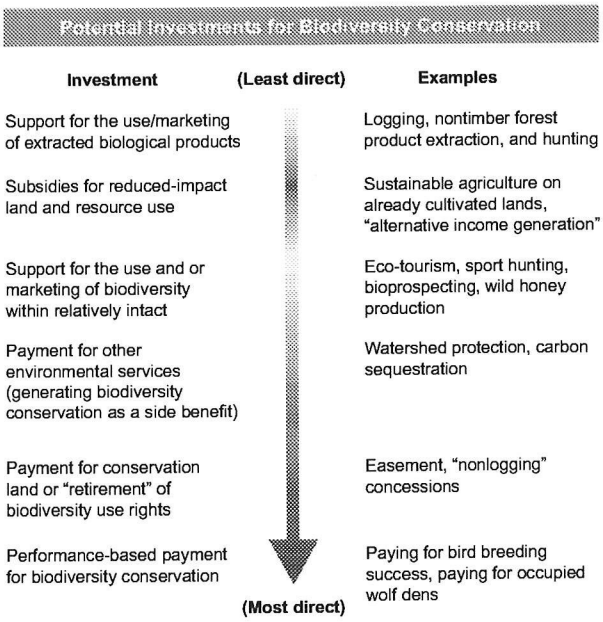
The international community has invested billions of dollars to stem the loss of biodiversity in developing nations (*1*, *2*). Despite these investments, the loss continues (*3*, *4*).

Biodiversity is a public good and thus is not supplied in sufficient quantities by individuals acting in their own self-interest. Conservation practitioners try to provide individuals who destroy ecosystems and species with incentives to preserve them. These incentives lie on a spectrum from indirect to direct with respect to their link with conservation objectives (see figure, this page). Conservation initiatives in the United States, Australia, and most of Europe increasingly emphasize more direct incentives: land purchases, leases, and easements, as well as financial incentives such as performance payments and tax relief. For example, the U.S. government spends over $1.7 billion per year to induce farmers to protect land (*5*), and The Nature Conservancy, with an annual budget of more than $700 million, operates almost exclusively through land purchases and easements (*6*, *7*).

These payment approaches are based on a willing buyer–willing seller model. Sellers deliver conservation outcomes in exchange for a negotiated payment in cash or in kind. Payments are conditional on conservation outcomes.

Conservation in developing nations has emphasized the more indirect end of the spectrum. Indirect approaches include initiatives like Integrated Conservation and Development Projects (ICDP) and Community-Based Natural Resource Management. Such projects encourage rural communities to maintain biodiversity by helping them to use it sustainably. They may also provide alternative sources of products, income, or social benefits (schools, wells, clinics, etc.) as a means of encouraging communities to cooperate. These kinds of efforts have been referred to as "conservation by distraction" (*8*).

After decades of global efforts to conserve biodiversity through indirect approaches, there is a growing recognition that such initiatives rarely work. Some authors (*9*, *10*) have pointed to basic conceptual flaws; for example, people are more likely to incorporate new sources of income as complements to existing activities rather than as substitutes for them. Others have noted that the technical, economic, social, and political conditions needed for an indirect approach to succeed are difficult to find in the real world (*11*, *12*). For conservation initiatives that encourage extractive activities (e.g., nontimber forest product collection), sustainability is a key concern (*13*–*15*). A recent review of ICDPs (*16*) declared that there was "a notable lack of successful and convincing cases where people's development needs have been effectively reconciled with protected area management."



Indirect Versus Direct Approaches

Potential obstacles to implementing a direct payment approach in developing nations include uncertain or inequitable land tenure, limited experience with and enforcement of legal contracts, and limited local opportunities for nonagricultural investment or employment. Direct payments may displace biodiversity loss to other areas, may be misappropriated or misused, and may create social conflict. However, these problems generally apply equally to indirect interventions.

Direct payments might be seen as a form of bribery or an imposition of Western values on developing nations. However, investments that encourage eco-tourism or create markets for tagua nuts are equally aimed at inducing rural communities to change their land use and livelihoods in response to Western values.

Recent debates (*17*) have highlighted four issues that need be examined in relation to direct and indirect approaches.

1) *Institutional complexity.* Indirect and direct approaches require institutions that can monitor ecosystem health, resolve conflict, coordinate individual behavior, and allocate and enforce rights and responsibilities. A system of conservation payments, however, allows practitioners to focus their energies on designing the requisite institutions. Existing direct payment initiatives have estimated administrative costs from 5% to 25% of the operating budget (*18*–*20*), whereas ICDPs have administrative costs at least as high, and often higher (*21*). A developing nation may not have the institutional capacity to make contractual agreements and to manage money in a direct payment initiative. If, however, it lacks such capacity, it would not likely have the institutional capacity to implement a more complex indirect intervention.

2) *Costs.* In general, a direct payment approach will be more cost-efficient than any indirect approach (*8*, *22*). For example, an analysis of a conservation intervention in southeastern Madagascar (*22*) indicates that, were the nearly $4 million of available conservation funds invested in annual payments conditional on the protection of forest, about 80% of the original forest could have been protected into perpetuity, whereas only 12% could have been protected through support of indirect incentives. Furthermore, rural residents receiving conservation payments would have received incomes two times those that could be generated through an indirect in-

P. J. Ferraro is with the Department of Economics, Andrew Young School of Policy Studies, Georgia State University, Atlanta, GA 30303–3084, USA. E-mail: pferraro@gsu.edu. A. Kiss is at the Environment and Social Development Unit, The World Bank, Washington, DC 20433, USA. E-mail: akiss@worldbank.org

tervention. The basic principle is that the cheapest way to get something you want is to pay for what you want (e.g., protected rain forest), rather than pay for something indirectly related to it (e.g., capital for improving eco-tourism), or more simply "you get what you pay for."

Paying people to protect habitat and wildlife can be surprisingly affordable. Many of the regions in which conservation practitioners work are at the margins of the economy where other land uses do not generate substantial net returns. For example, the middle-income nation of Costa Rica pays rural residents about $35 annually per hectare of forest protected, and excess demand for conservation contracts suggests that these payments are higher than necessary (*23*). Even cheaper, Conservation International is protecting 81,000 hectares of rain forest in Guyana through a conservation concession that costs $1.25 per hectare per year (*24*), and The Wildlife Foundation in Kenya is securing migration corridors on private land through conservation leases at $4 per acre per year (*25*, *26*).

We are not arguing against short-term assistance for profitable, eco-friendly activities that can protect biodiversity. Conservation practitioners and donors, however, must ask themselves why external assistance is necessary if these activities are so profitable (*27*). Rural residents may face credit constraints, misunderstand the benefits conservation would afford them, or be unable to organize to realize the benefits, but we suspect that such conditions are rarely the main constraints.

3) *Development benefits*. The indirect approach is attractive to many stakeholders because it seems to achieve conservation and development objectives simultaneously (despite evidence suggesting it achieves neither in most cases). However, direct payments benefit poor farmers by improving cash flows, providing a fungible store of wealth, and diversifying sources of household income. Furthermore, under a payment approach, the land holders/resource users decide how best to meet their own goals and aspirations, rather than being subsidized to carry out predetermined activities as is the case under the indirect approach.

Paying an individual or community for "not doing something" might be seen as a form of social welfare rather than development. However, the idea that conservation payments are a form of welfare belies what conservationists have been arguing for decades: Biodiversity is a valuable commodity and biodiversity protection is an alternative land use.

4) *Sustainability*. The Holy Grail for the international conservation community is the self-financing conservation activity. Direct payments are seen as undesirable because they require an ongoing financial commitment to maintain the link between the investment and the conservation objectives. Like the legendary Holy Grail, however, the self-financing conservation activity is elusive. Indirect approaches are also likely to require a sustained flow of funds over time. A recent World Bank analysis of ICDPs (*16*) argued that conservation initiatives "based on simplistic ideas of making limited short-term investments in local development and then hoping this will somehow translate into sustainable resource use and less pressure on parks need to be abandoned."

Future Prospects

Direct payment initiatives are rare in developing nations, but conservation pioneers are experimenting with them. A recent symposium (*17*) highlighted the use of forest protection payments in Costa Rica, conservation leases for wildlife migration corridors in Kenya, conservation concessions on forest tracts in Guyana, and performance payments for endangered predators and their prey in Mongolia. South Africa and American Samoa have over a decade of experience with "contractual national parks," which are leased from communities. Other payment initiatives are being designed or are under way in Mexico, El Salvador, Colombia, Honduras, Guatemala, Panama, Russia, and Madagascar (*28*). Payments can be made for protecting entire ecosystems or specific species, with diverse institutional arrangements existing among governments, firms, mutilateral donors, communities, and individuals.

Direct payment approaches are not "silver bullets" that can be applied immediately and easily in all situations. Furthermore, broader policy interventions, such as removing perverse direct and indirect subsidies that encourage the loss of habitats and their biodiversity (*29*, *30*), are also needed. However, people will generally do what is in their own interest, particularly their short-term interest. If they can receive more benefits from clearing an area of habitat than they could from protecting it, they will clear it. A society would never think to provide a public good like national defense through indirect means. The conservation community must reconsider its attempts to provide biodiversity through indirect means. If we want to get what we pay for, we must start tying our investments directly to our goals.

References and Notes

1. J. Hardner, R. Rice, *Sci. Am.* (May), 89 (2002).
2. A. James *et al.*, *BioScience* **51**, 43 (2001).
3. F. Achard *et al.*, *Science* **297**, 999 (2002).
4. A. Balmford et al., *Science* **297**, 950 (2002).
5. *FY 2001 Budget Summary* (U.S. Department of Agriculture Washington, DC, 2001); available at www.usda.gov/agency/obpa/Budget-Summary/2001/text.htm
6. *2001 Annual Report* (Nature Conservancy Washington, DC, 2002); available at http://nature.org/aboutus/annualreport2001/.
7. More examples can be found at http://epp.gsu.edu/pferraro/special/special.htm.
8. P. J. Ferraro, R. D. Simpson, *Land Econ.* **78**, 339 (2002).
9. P. J. Ferraro, *Conserv. Biol.* **15**, 990 (2001).
10. A. Kiss, "Making biodiversity conservation a land use priority," in *Getting Biodiversity Projects to Work: Towards More Effective Conservation and Development*, T. McShane and M. Wells, eds. (Columbia Univ. Press, New York, in press).
11. N. Salafsky *et al.*, *Evaluating Linkages Between Business, the Environment, and Local Communities: Final Analytical Results from the Biodiversity Conservation Network* (Biodiversity Support Program, Washington, DC, 1999).
12. D. Roe *et al.*, *Evaluating Eden: Exploring the Myths and Realities of Community-Based Wildlife Management* [Series No. 8, International Institute for Environment and Development (IIED) Publications, London, 2001], 62 pp.
13. D. D. Tewari, J. Y. Campbell, *Unasylva* **187**, 26 (1996).
14. C. B. Barrett, P. Arcese, *Land Econ.* **74**, 449 (1998).
15. S. Norris, N. L. Chao, *Conserv. Pract.* **3**, 30 (2002).
16. M. Wells *et al.*, *Investing in Biodiversity: A Review of Indonesia's Integrated Conservation and Development Projects* (East Asia Region, World Bank, Washington, DC, 1998).
17. Direct Payments as an Alternative Conservation Investment, a symposium at the 16th Annual Meetings of the Society for Conservation Biology, Canterbury, England, 15 July 2002. For more detail, see http://epp.gsu.edu/pferraro/special/special.htm.
18. "Project appraisal document on a proposed IBRD loan of US$32.6 million to the Republic of Costa Rica and a grant from the Global Environment Facility Trust Fund of SDR 6.1 million (US$8 million equivalent) to the National Forestry Financing Fund for the Ecomarkets Project," San Jose, Costa Rica,15 May 2000 (Central American Department, Latin America and the Caribbean Regional Office, World Bank, Washington, DC, 2000).
19. E. Ortiz, Instituto Tecnológico de Costa Rica, personal communication.
20. "The environmental effects of agricultural land diversion schemes" [Organization for Economic Cooperation and Development (OECD), Paris, 1997].
21. J. Peters, *J. Agric. Environ. Ethics* **11**, 17 (1998). Peters, a former consultant to an African ICDP, estimated that 55% of his ICDP's budget went to U.S.-based administrative overhead and expatriate technical consultants, which is a common outcome among ICDPs. Only 2% of the budget went to rural residents living around the endangered rain forest ecosystem.
22. J. C. Conrad, P. J. Ferraro, "Habitat conservation: The dynamics of direct and indirect payments" (Environmental Policy Working Paper Ser. 2001-005, Andrew Young School of Policy Studies, Georgia State University, Atlanta, GA, 2001); available at http://epp.gsu.edu/pferraro/docs/ConradFerraroWorkingPaper2001Distrib.pdf
23. E. Ortiz, paper presented at the symposium, Direct Payments as an Alternative Conservation Investment (*17*).
24. R. Rice, paper presented at the symposium, Direct Payments as an Alternative Conservation Investment (*17*).
25. H. Gichohi, paper presented at the symposium Direct Payments as an Alternative Conservation Investment (*17*).
26. R. E. Gullison *et al.*, *Nature* **404**, 923 (2000) for other examples of inexpensive payment initiatives.
27. P. J. Ferraro, R. D. Simpson, *Resources* **143**, 17 (2001).
28. For more details and examples, see (*10*) and http://epp.gsu.edu/pferraro/special/special.htm.
29. N. Myers, J. Kent, *Perverse Subsidies* (Island Press, Washington, DC, 2001).
30. S. L. Pimm *et al.*, *Science* **293**, 2207 (2001).