

Global contribution of echinoderms to the marine carbon cycle: CaCO₃ budget and benthic compartments

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Abstract. The contribution of carbonate-producing benthic organisms to the global marine carbon budget has been overlooked, the prevailing view being that calcium carbonate (CaCO₃) is predominantly produced and exported by marine plankton in the “biological pump.” Here, we provide the first estimation of the global contribution of echinoderms to the marine inorganic and organic carbon cycle, based on organism-level measurements from species of the five echinoderm classes. Echinoderms’ global CaCO₃ contribution amounts to ~0.861 Pg CaCO₃/yr (0.102 Pg C/yr of inorganic carbon) as a production rate, and ~2.11 Pg CaCO₃ (0.25 Pg C of inorganic carbon) as a standing stock from the shelves, slopes, and abyssal depths. Echinoderm inorganic carbon production (0.102 Pg C/yr) is less than the global pelagic production (0.4–1.8 Pg C/yr) and similar to the estimates for carbonate shelves globally (0.024–0.120 Pg C/yr). Echinoderm CaCO₃ production per unit area is ~27.01 g CaCO₃·m⁻²·yr⁻¹ (3.24 g C·m⁻²·yr⁻¹ as inorganic carbon) on a global scale for all areas, with a standing stock of ~63.34 g CaCO₃/m² (7.60 g C/m² as inorganic carbon), and ~7.97 g C/m² as organic carbon. The shelf production alone is 77.91 g CaCO₃·m⁻²·yr⁻¹ (9.35 g C·m⁻²·yr⁻¹ as inorganic carbon) in contrast to 2.05 g CaCO₃·m⁻²·yr⁻¹ (0.24 g C·m⁻²·yr⁻¹ as inorganic carbon) for the slope on a global scale. The biogeography of the CaCO₃ standing stocks of echinoderms showed strong latitudinal variability. More than 80% of the global CaCO₃ production from echinoderms occurs between 0 and 800 m, with the highest contribution attributed to the shelf and upper slope. We provide a global distribution of echinoderm populations in the context of global calcite saturation horizons, since undersaturated waters with respect to mineral phases are surfacing. This shallowing is a direct consequence of ocean acidification, and in some places it may reach the shelf and upper slope permanently, where the highest CaCO₃ standing stocks from echinoderms originate. These organism-level data contribute substantially to the assessment of global carbonate inventories, which at present are poorly estimated. Additionally, it is desirable to include these benthic compartments in coupled global biogeochemical models representing the “biological pump” and its feedbacks, since at present all efforts have focused on pelagic processes, dominated by coccolithophores. The omission of the benthic processes from modeling will only diminish the understanding of elemental fluxes at large scales and any future prediction of climate change scenarios.

Key words: benthic compartments; CaCO₃ budget; carbon cycle; carbonate production; echinoderms; ocean acidification; standing stock.

INTRODUCTION

Global significance of echinoderms: a critical role in the marine CaCO₃ cycle

The Echinodermata constitute a quantitatively important carbonate-producing marine phylum (Weber 1969), dominating numerous soft and hard bottom

ecosystems in the world’s oceans at all depths (McClintock 1994), where they are often the predominant grazer (Lawrence 2007). Echinoderms are divided into five classes: Asterozoa, Echinozoa, Ophiurozoa, Holothurozoa, and Crinozoa, which are found from the intertidal to the deep sea (Gage and Tyler 1991, Ellis and Rogers 2000). Asterozoa establish dense populations over extensive geographical and bathymetric ranges (see Franz et al. 1981, Sloan and Aldridge 1981, Howell et al. 2002). Echinozoa frequently populate littoral and sublittoral zones (Turon et al. 1995), and the shelf and slope areas with species-specific bathymetric ranges (e.g., Gutt 1991). Ophiurozoa are

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particularly abundant at bathyal depths (Smith and Hamilton 1983, Haedrich and Maunder 1984, Fujita and Ohta 1989, 1990, Piepenburg and Schmid 1996). Holothuroidea are common dwellers of soft sediments especially in the deep sea in all oceans (Gutt 1988, Billett 1991, Billett et al. 2001). Lastly, the Crinoidea are the least studied class, some of which are largely benthopelagic, with certain species restricted to the deep sea (Tokeshi 2002), while others dominate shallow tropical coral reefs (Messing 1994). This ubiquitous presence of echinoderms in all oceans and latitudes, especially on the neritic, shelf, and slope areas, indicates a critical role in calcium carbonate (CaCO_3) production and sedimentation processes, which has been widely ignored to date.

A reliable assessment of the role of neritic CaCO_3 in the carbon cycle is still in its infancy (see Ridgwell and Zeebe 2005), with large gaps in the understanding of the contemporary global carbon budget that regulates large-scale processes (Schlesinger 1997). Within the global carbon budget, processes in the continental shelf are poorly understood in terms of carbonate production and accumulation (Milliman and Droxler 1995). Biologically mediated reactions (precipitation and dissolution of CaCO_3) contribute significantly to the global CO_2 balance (Berelson et al. 2007, Doney et al. 2009), as the calcification process shifts the seawater carbonate equilibrium, producing dissolved CO_2 (Wollast et al. 1980). Approximately 0.6 moles of CO_2 are released to the seawater with the secretion of one mole of CaCO_3 at a temperature of 25°C ($\text{Ca}^{2+} + 2\text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$) (Ware et al. 1992).

The role of CaCO_3 production in marine ecosystems has been studied in detail for coral reefs (Gattuso et al. 1998), coccolithophores (Westbroek et al. 1989), Halimeda bioherms (Rees et al. 2007), the pelagic realm (Lee 2001), and in limited detail for the continental shelves and slopes (Milliman and Droxler 1995, Iglesias-Rodriguez et al. 2002). Shelf and slope environments, where high echinoderm biomass occurs, have been poorly sampled in terms of CaCO_3 production and accumulation, with present estimations having uncertainties of up to 100% (Iglesias-Rodriguez et al. 2002). Additionally, the CaCO_3 compartment on production and export that is included in global formulations of coupled biogeochemical models of the “biological pump” only accounts for pelagic processes mainly concerning the calcite of coccolithophores (with an exclusive focus in *Emiliania huxleyi*; e.g., Gehlen et al. 2007), and to a lesser extent the aragonite of pteropods (e.g., Gangstø et al. 2008). An omission of coupled benthic compartments in the biological pump, including the echinoderm’s budget, may compromise the outcomes of these models and future predictions.

Yet, quantitative studies on regional benthic CaCO_3 budgets at the organism-level are scarce (Smith 1972, Collins 1986). For echinoderms, the available CaCO_3 production data are for an ophiuroid in the English Channel ($682 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; Migne et al. 1998) and

for a suite of echinoderms off California, between 20 and $336 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Smith 1972).

The contribution of echinoderms in the benthic compartment of the global CaCO_3 cycle is important for three reasons: (1) echinoderms incorporate calcium (Ca) and magnesium (Mg) into single crystals of magnesium containing calcite after the pluteus stage of development (as larvae) (see Politi et al. 2004 and references therein) in a varying ratio related to the concentrations in the water (Weber 1969, Dickson 2002), storing high amounts of CaCO_3 ; (2) echinoderm populations typically attain high biomass in the neritic, shelf, and slope environment (Ellis and Rogers 2000, Metaxas and Giffin 2004), and are widely present, dominating the abyssal plains (Gage and Tyler 1991, Ruhl 2007), bearing a substantial CaCO_3 standing stock over large areas (Migne et al. 1998); and (3) the carbon stored in echinoderms is directly released to the benthic system when they die. Mortality occurs year round as a result of a natural process (Rees and Dare 1993), or it can happen in mass mortality events (Lessios et al. 1984a, b).

Echinoderm CaCO_3 contribution at risk: ocean acidification

Ocean acidification is predicted to occur under current IPCC CO_2 emissions scenarios (Houghton et al. 2001). Around 50% of the emissions of CO_2 are being absorbed by the oceans, increasing the pCO_2 with a concomitant decrease in the surface pH by 0.3–0.4 units by the end of the century (Feely et al. 2004, Caldeira and Wickett 2005, Orr et al. 2005). At present, the CO_2 interaction with seawater reduces the carbonate ion concentration, which is thought to regulate the calcification of extracellularly calcifying organisms (Spero et al. 1997, Marubini et al. 2008). This process is governed by the CaCO_3 saturation state ($\Omega = (\text{CO}_3^{2-})(\text{Ca}^{2+})/K_{\text{sp}}^*$), where K_{sp}^* is the apparent stoichiometric solubility product. For values of $\Omega < 1$ (undersaturated), seawater is corrosive, and dissolution may proceed (Isaji 1995). It should be noted that for organisms bearing magnesium, such as echinoderms, the saturation state may be lower due to the higher solubility of the Mg mineral (see Morse et al. 2006 for calculations). At present CO_2 concentrations, for an echinoderm with a 10% mineralogy of MgCO_3 , the saturation state (Ω) with respect to its mineralogy (Ω_{Mg} ; Morse et al. 2006, Andersson et al. 2008) is more than one unit lower than only with respect to calcite (Lebrato et al. 2009).

Saturation horizons with respect to all mineral phases (including Mg-bearing calcites) are migrating toward the surface (Feely et al. 2004, Morse et al. 2006, Andersson et al. 2008, Tyrrell et al. 2008), especially in the Pacific Ocean (Feely et al. 2008), potentially risking the survival of calcifiers in the neritic, shelf, and slope environments (see Millero et al. [1979] for the special situation in the Mediterranean Sea). Orr et al. (2005) predicted that by 2100 the Southern and the Arctic Oceans could be undersaturated with respect to aragonite, and then

calcite would follow in ~50–100 years. This has also major implications for calcifying taxa at those latitudes.

Organism-level responses are still poorly understood (Fabry et al. 2008, Doney et al. 2009). Studies on the effects on echinoderms are still in their infancy, but preliminary work suggests morphological failure (Kurihara and Shirayama 2004) and a decrease in the amount of CaCO_3 incorporated (Clark et al. 2009) (as seen for molluscs in Gazeau et al. [2007]). However, the main concern is a failure of planktonic larvae to recruit to adult populations due to the effect of changing water carbonate chemistry and rising temperatures on the onset of calcification in larvae (long-term reduction in the CaCO_3 contribution). Abnormal skeletogenesis and 100% mortality has been recorded in ophiuroid larvae under pH conditions that were set at 0.2 units lower than present values (Dupont et al. 2008). Reduced larval survival has also been found in echinoid, ophiuroid, and asteroid larvae cultured under high CO_2 conditions (Byrne and Davis 2008; see Dupont and Thorndyke 2009 for details). Yet, emerging work suggests that there are fundamental gaps preventing us from understanding the effect of acidification, with some examples of completely contrary responses to enhanced CO_2 conditions (Ries et al. 2008, Wood et al. 2008, Dupont and Thorndyke 2009). Experiments combining CO_2 with temperature in multifactorial approaches show even more complex responses. While Gooding et al. (2009) report an increase in growth of an adult starfish at high CO_2 and high temperature, Byrne et al. (2009) show that elevated CO_2 has no major effect on sea urchin early stages, but that temperature deeply reduces gastrulation success and impairs early development. Echinoderms do incorporate high-magnesium calcite, which is more susceptible to dissolution than other skeletons formed only of calcite or aragonite (Bertram et al. 1991). The consequence of this is a higher susceptibility to undersaturation with respect to this mineral phase in the water (Morse et al. 2006). Moreover, during larval stages, unstable, transient, amorphous CaCO_3 is formed and is more soluble than the other compounds (Raz et al. 2003). This may impede optimum biomineralization processes at early developmental stages that could impact upon the pool of adult populations and their contribution to the carbon cycle.

This study focuses on the measurement of organic and inorganic carbon in a suite of species from the five echinoderm classes to provide the first estimation of their contribution to the benthic compartment of the oceanic CaCO_3 budget. This contribution is examined both in terms of a standing stock (“static term”) and a production rate (“rate term”). We also address the global distribution of the echinoderm adult populations and put this into perspective with the present-day CaCO_3 saturation horizons. Our work highlights the poor understanding of large-scale carbon processes associated with calcifying taxa such as echinoderms and tackles some of the uncertainties in the CaCO_3

budget in neritic zones, shelves, and slopes. The results and conclusions of this work draw attention to the need for a major reassessment of the contribution of benthic organisms such as echinoderms to the global marine CaCO_3 cycle, and the incorporation of a benthic compartment in coupled global biogeochemical models of the biological pump, beyond the traditional pelagic processes.

ECHINODERMS CARBON MEASUREMENTS

Samples origin and treatment

Fresh echinoderm samples were collected in the Atlantic Ocean at different latitudes, with collection methodologies including vessel-based and manual sampling (Table 1). Representatives from the five echinoderm classes were analyzed (Table 1). The number of individuals per species depended on the availability of material. In the case of deep-sea samples, few individuals were available (three per species), while in shallow water surveys, between three and 14 individuals per species were collected (Table 2). All individuals analyzed were selected according to size to ensure that the main representative size classes for adults were included. Samples used for analysis had all their body parts intact, including spines in the case of echinoids. Samples with missing components or severe damage were excluded. All material was carefully cleaned to exclude any calcareous encrustations and sediment. All samples were sealed in individual plastic bags and stored at -80°C .

Carbon estimations

All echinoderm samples were transferred from -80°C to a freeze dryer within their respective plastic bags (Harris 1954). Samples were freeze dried continuously for 48 hours and subsequently disintegrated to a homogeneous powder with a rotating metal blade. Carbon analyses were performed in triplicate for inorganic carbon (IC) and for total carbon (TC) using Model 5012 UIC Coulometers (UIC Coulometrics, Joliet, Illinois, USA; Johnson 1995, Johnson et al. 1998). The amount of echinoderm sample used in the subsample measurements was $16.08 \text{ mg} \pm 4.01$ ($n = 174$) for IC, and $11.55 \text{ mg} \pm 2.56$ (mean \pm SD; $n = 174$) for TC. Calibration of the Coulometers was verified with pure, dry CaCO_3 standards. IC content was determined to be $11.94\% \pm 0.12\%$ (cf. 12.00%), equivalent to $99.55\% \pm 1.01\% \text{ CaCO}_3$ ($n = 16$). TC content of the standard was determined to be $11.98\% \pm 0.01\%$ (cf. 12.00%), equivalent to $99.85\% \pm 0.81\% \text{ CaCO}_3$ ($n = 8$). Organic carbon (OC) was calculated as the difference between TC and IC.

The carbon fraction representing CaCO_3 was assumed to be almost equal to the IC (Davoult et al. 1992). Thus, the CaCO_3 content was a function of the IC: CaCO_3 percentage = $(\text{IC}\% \times 8.33)$, where 8.33 is the CaCO_3/C ratio based on the elemental atomic mass. We assumed that the IC present as MgCO_3 made a negligible contribution to the total although the proportion of

TABLE 1. Echinoderm samples used as model organisms along with sampling survey details.

Class and species	Sample depth	Collection method	Location coordinates	Location name
Asteroidea				
<i>Asterina gibbosa</i>	intertidal	manual	50.63° N, 2.39° W	English Channel (NE Atlantic)
<i>Asterias rubens</i>	intertidal	manual	53.24° N, 4.46° W	Swansea (NE Atlantic)
<i>Marthasterias glacialis</i>	intertidal	manual	43.58° N, 6.24° W	Cape Vidio (NE Atlantic)
<i>Zoroaster fulgens</i>	1131–1156 m	semi-otter trawl collection	49.28° N, 12.36° W	Porcupine Sea Bight (NE Atlantic)
Echinoidea				
<i>Cidaris blakei</i>	595 m	submersible collection	24.83° N, 77.50° W	South West Reef (NW Atlantic)
<i>Paracentrotus lividus</i>	intertidal	manual	43.58° N, 6.24° W	Cape Vidio (NE Atlantic)
<i>Psammechinus miliaris</i>	intertidal	manual	50.35° N, 4.13° W	Plymouth (NE Atlantic)
<i>Tripneustes ventricosus</i>	subtidal	manual	25.12° N, 77.29° W	Paradise Island (NW Atlantic)
Ophiuroidea				
<i>Ophiosium lymani</i>	1131–1156 m	semi-otter trawl collection	49.20° N, 12.30° W	Porcupine Sea Bight (NE Atlantic)
Holothuroidea				
<i>Holothuria forskali</i>	intertidal	manual	43.58° N, 6.24° W	Cape Vidio (NE Atlantic)
Crinoidea				
<i>Antedon mediterranea</i>	63 m	bottom trawl collection	41.43° N, 2.32° W	Catalan Slope (Mediterranean Sea)

CaCO₃ and MgCO₃ depends on the class and is mainly species-specific (Vinogradov 1953, Weber 1969). The proportions of MgCO₃, which can attain between 5% and 18% of the dry skeleton mass alone or single skeletal parts (see Vinogradov 1953), represent an overestimation when considering whole bodies of echinoderms with all the CaCO₃ and the organic carbon. The contribution in terms of MgCO₃ was not included in our CaCO₃ budget analysis. Yet, the separate contribution of

CaCO₃ and MgCO₃ to the global budget is being reassessed with samples used in this study as well as with new ones from the equator, the Arctic, and the Southern Ocean (Antarctica) (J. Ries and M. Lebrato, *unpublished manuscript*).

Echinoderm global carbon data set

Data compilation.—Field data were compiled from the literature and two unpublished data sets (Appendix:

TABLE 2. Regression equations fitted to the collected-samples data to allow conversions from size (*S*) to dry mass of an average adult (also included are general equations used for literature data).

Species or class	No. samples	Equation for dry mass	<i>r</i> ²	<i>S</i> definition†	Dry mass/wet mass (%)
<i>Asterina gibbosa</i>	10	= (0.079 × <i>S</i>) – (0.101)	0.98	center disk to arm tip	44.18
<i>Asterias rubens</i>	8	= (0.797 × <i>S</i>) – (40.114)	0.77	center disk to arm tip	24.73
<i>Marthasterias glacialis</i>	7	= (0.409 × <i>S</i>) – (7.633)	0.79	center disk to arm tip	33.00
<i>Zoroaster fulgens</i>	4	= (0.301 × <i>S</i>) – (10.314)	0.98	center disk to arm tip	61.05
<i>Cidaris blakei</i>	3	see Echinoidea	0.84	test diameter	44.19
<i>Paracentrotus lividus</i>	14	= (0.808 × <i>S</i>) – (20.168)	0.90	test diameter	40.61
<i>Psammechinus miliaris</i>	14	= (0.554 × <i>S</i>) – (10.621)	0.99	test diameter	38.07
<i>Tripneustes ventricosus</i>	3	see Echinoidea	0.84	test diameter	18.80
<i>Ophiosium lymani</i>	6	= (0.027 × <i>S</i>) – (0.611)	0.83	center disk to arm tip	88.19‡
<i>Ophiosium lymani</i>	6	= (0.149 × <i>S</i>) – (1.007)	0.72	disk diameter	88.19‡
<i>Holothuria forskali</i>	3	= (0.067 × <i>S</i>) – (1.371)	0.99	body length	11.06
<i>Antedon mediterranea</i>	3	= (0.052 × <i>S</i>) – (0.727)	0.72	center disk to arm tip	43.07
<i>Antedon mediterranea</i>	3	= (0.200 × <i>S</i>) – (0.070)	0.95	disk diameter	43.07
Asteroidea	32	= (0.309 × <i>S</i>) – (2.518)	0.83	center disk to arm tip	32.90§
Echinoidea	36	= (0.492 × <i>S</i>) – (8.202)	0.84	test diameter	34.02
Ophiuroidea	12	= (0.038 × <i>S</i>) – (0.320)	0.88	center disk to arm tip	47.10§
Ophiuroidea	12	= (0.136 × <i>S</i>) – (0.949)	0.86	disk diameter	47.10§
Holothuroidea	3	= (0.067 × <i>S</i>) – (0.070)	0.99	body length	19.30§
Crinoidea	3	= (0.052 × <i>S</i>) – (0.727)	0.72	center disk to arm tip	43.07
Crinoidea	3	= (0.200 × <i>S</i>) – (0.070)	0.95	disk diameter	43.07

Note: Dry mass to wet mass conversions used both in samples and biomass data are also presented (for literature data, also).

† Size measured with knife-edged calipers. Two types of size (*S*) estimation were used for the Ophiuroidea and Crinoidea.

‡ Value likely to have been affected by a freezing issue.

§ Value recommended by Ricciardi and Bourget (1998).

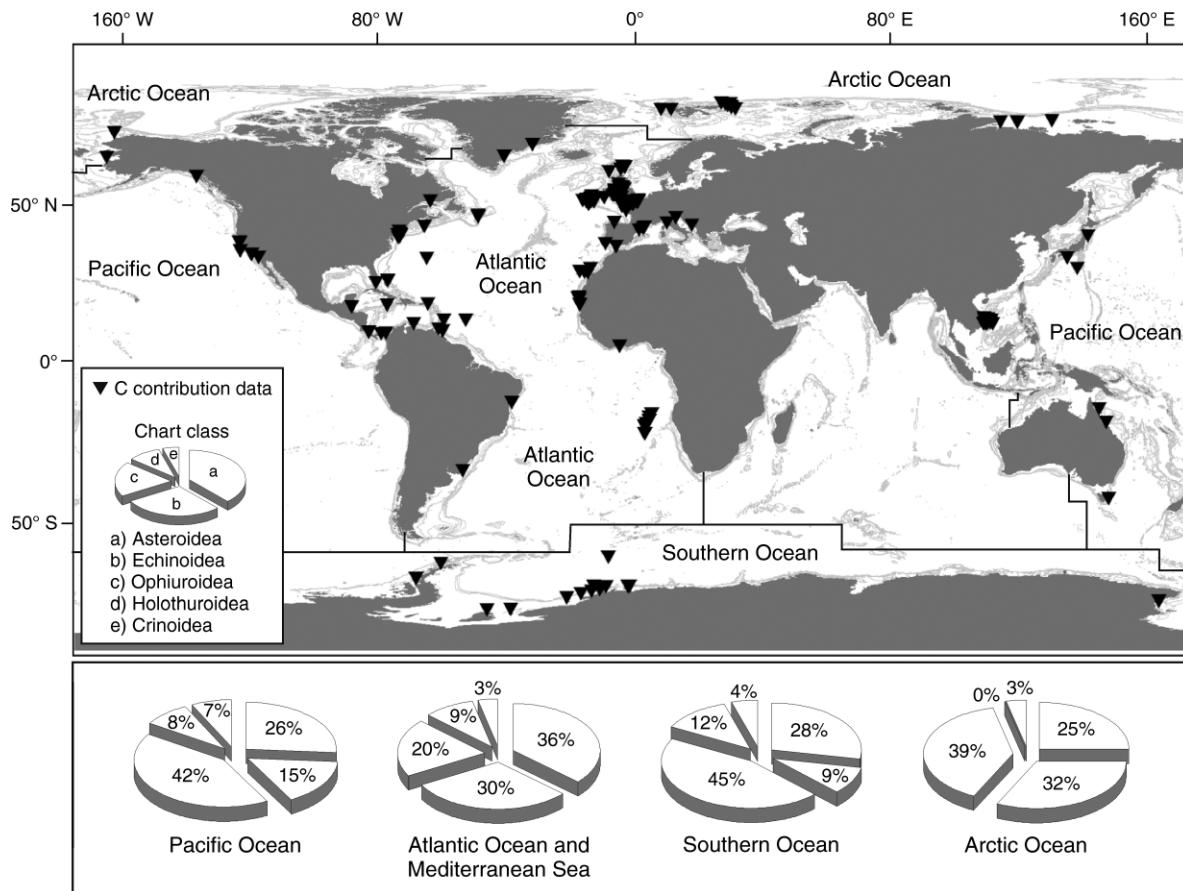


FIG. 1. Echinoderm distribution data from the literature used to estimate the echinoderm global carbon contribution ($n = 523$ sites). For each ocean basin, the percentage contribution of each class is included in the pie charts. The echinoderm class labels in all charts follow the sequence (a–e) of those shown in the pie chart in the inset of the map. Bathymetric data range from 100 to 2000 m. Gridded data were taken from the general bathymetric chart of the oceans (GEBCO) Digital Atlas (IOC et al. 2003).

Table A1) when three conditions were met: (1) the echinoderm data were species specific or class specific (papers just including a general “echinoderms” term were excluded), (2) a density and/or biomass estimation (dry or wet) was available (Appendix: Table A1), and (3) geographical information (latitude and longitude) was available. Additional information included the depth of the density/biomass estimation, a size reference, the areal extent occupied at such density/biomass, and any annual mortality rate. The field sampling methodology was also recorded (Appendix: Table A1). Field surveys varied from visual counts with quadrates, to trawls and submersible photographs. The final data set was intended to represent all oceans and latitudes (Fig. 1), but it is biased toward the Atlantic Ocean. The low latitudes, the Indian Ocean, southeast and west Pacific, and African coasts are greatly undersampled (Fig. 1). The most northern samples were from the Barents Sea (80°57' N, 27°14' E), while the most southern originated in the Weddell Sea (77°30' S, 46°0' W). The deepest data correspond to the Angola Basin at 5497 m and a suite of other records in the northeast Atlantic and northeast Pacific from 3000 to >4000 m.

Shallow water samples come from all oceans starting in the intertidal environment.

Standing stocks and production rates calculation.—The majority of the literature data had only a density value recorded (e.g., number of individuals per unit area), and intermediate steps were taken to translate density to biomass estimations, carbon standing stocks, and production rates. Regression equations enabled to convert size (S) for a mean adult to dry mass using data from the species analyzed (Table 2). Equations for each species and class were in the form of dry mass = $(a \times S) - b$, where a is the intercept, b is the gradient, and S is a representative size measurement. Size was derived from published data (Weber 1968, Barnes et al. 1976, Russo 1980, Lewis and Storey 1984, Gutt 1988, Brey and Gutt 1991, Gutt and Klages 1991, Kenner and Lares 1991, Clark and Downey 1992, Ebert and Russell 1992, Sala et al. 1998, Chiappone et al. 2002, McCarthy and Young 2002, Griffin et al. 2003, Pearce et al. 2005). From the estimated dry mass of the species, the dry biomass was a function of the recorded density and the mean dry mass of an adult.

TABLE 3. Organic carbon percentage (OC%), inorganic carbon percentage (IC%), and CaCO₃ percentage (CaCO₃%), mean ± SD, for sample species used as model organisms.

Species or class	n†	OC%	IC%‡	CaCO ₃ %
<i>Asterina gibbosa</i>	6	12.93 ± 3.61	7.35 ± 0.83	61.25 ± 6.95
<i>Asterias rubens</i>	8	18.75 ± 5.37	5.85 ± 1.03	48.78 ± 8.61
<i>Marthasterias glacialis</i>	7	17.36 ± 3.11	6.49 ± 0.90	54.98 ± 7.55
<i>Zoroaster fulgens</i>	4	9.64 ± 0.52	8.96 ± 0.54	74.64 ± 4.53
<i>Cidaris blakei</i>	3	2.32 ± 0.56	10.42 ± 0.17	86.83 ± 1.42
<i>Paracentrotus lividus</i>	8	7.53 ± 1.08	8.95 ± 0.24	74.63 ± 2.02
<i>Psammechinus miliaris</i>	8	4.88 ± 0.98	9.69 ± 0.34	80.71 ± 2.85
<i>Tripneustes ventricosus</i>	3	7.40 ± 0.07	7.61 ± 0.23	63.42 ± 1.98
<i>Ophiosium lymani</i>	6	5.98 ± 0.63	9.35 ± 0.14	77.91 ± 1.24
<i>Holothuria forskali</i>	3	27.44 ± 2.01	0.41 ± 0.13	3.46 ± 1.09
<i>Antedon mediterranea</i>	3	8.48 ± 1.13	8.74 ± 0.16	72.86 ± 1.36
Asteroidea	4	14.67§	7.16§	59.69§
Echinoidea	2	4.86¶	9.01¶	75.12¶
Echinoidea	2	6.21#	9.32#	77.67#
Ophiuroidea	1	5.98§	9.35§	77.91§
Holothuroidea	1	27.44§	0.41§	3.46§
Crinoidea	1	8.48§	8.74§	72.86§

Note: Also included are the general carbon percentages applied to other species compiled from studies in the literature.

† Represents either the number of individuals per sample species or the number of sample species included per class used to extrapolate to other literature studies.

‡ Inorganic carbon in echinoderms is stored as CaCO₃, MgCO₃, and high-Mg CaCO₃ (Weber 1969, Dickson 2002).

§ Data for all latitudes.

¶ Data for equatorial latitudes.

Data for all latitudes except equatorial.

Data points with biomass estimations were divided between wet and dry values. Wet mass values were converted to dry by using either published dry mass/wet mass percentage conversions (Ricciardi and Bourget 1998) or measurements from the laboratory (Table 2). Dry biomass data were used directly (few cases). Original data that were not estimated per square meter were normalized to this unit (m²) for comparability. All other data converted through the dry or wet mass protocol were eventually in the form of dry biomass per square meter. The calculation of the standing stock of carbon was the product of the dry biomass and a standard carbon percentage (OC, IC, and CaCO₃). Carbon data for the species analyzed were extrapolated to all literature data in all oceans (see *Results* and Table 3; for limitations see *Echinoderms carbon measurements: Echinoderm global carbon data set: Limitations in the extrapolation of carbon and mortality conversions globally*).

The conversion of standing stocks to production rates was based on the data from Smith (1972), which used in situ data from the CaCO₃ mass of live echinoderms per unit area ("calciass") to assess the production rates off California, USA. We refer to this calciass term here for echinoderms as "CaCO₃ standing stock" in grams of CaCO₃ per square meter. In order to convert the calculated CaCO₃ standing stocks to production, we used a rate factor (referred to as "turnover"). The standing stocks are a "static term," while the turnover is a "rate term"; the product of the two is the "production rate" for the purpose of this paper. Haderlie (1969) provided a model to assess organism's turnover rate, which is a function of the continual growth and the time to achieve

a limiting size. It assumes that organisms (in this case echinoderms) grow to this limiting size and then they die (see Smith [1972] and Haderlie [1969] for the mathematical details). Thus, growth and size distribution data can be used to work out mortality based on the assumption that mortality is constant (at a limiting size), growth follows the von Bertalanffy equation (von Bertalanffy 1938), and recruitment is constant (see Smith 1972).

For the purpose of our global calculations we used a turnover rate from the standing stock of 0.2 yr⁻¹ for ophiuroids, 1.0 yr⁻¹ for echinoids, and 0.3 yr⁻¹ for the rest (see details for specific species in Smith [1972] and references therein). The work of Smith (1972) was done off southern California, from 32° to 34° N, in waters between 10° and 20°C, and depths between 0 and 22 m. The conversion factors used for echinoderms in this study (turnover rate) may be valid for many temperate neritic and shelf environments globally, since the original authors derived their data from those areas. However, they represent an extrapolation to the echinoderms' turnover rates in the slopes, the bathyal depths, and certainly for the low latitudes.

The ability of this data set to predict the total carbon contribution of echinoderms to the carbon cycle is limited, since we do not know the global area they occupy. However, it is a useful approximation per unit area based on the amount of data collected. In order to provide conservative global carbon figures both as standing stocks and production rates, the area occupied by the shelves, slopes, and the abyssal depths published in Iglesias-Rodriguez et al. (2002) and in Milliman

(1993) were used in combination with the calculated data. We also used data on the depth range of the shelf, slope, an abyssal depths from Gage and Tyler (1991) and Anikouche and Sternberg (1973) to derive specific standing stocks and production rates at those areas. For the shelf we used an area of $10 \times 10^{12} \text{ m}^2$ (from 0 to 200 m), for the slope an area of $32 \times 10^{12} \text{ m}^2$ (200 to 2000 m), and for the abyssal depths (including the continental rise) an area of $290 \times 10^{12} \text{ m}^2$ ($>2000 \text{ m}$). For the shelf depth range, we ignored that in Antarctica it is deeper compared with other shelves worldwide with a mean water depth of 350 m (Picken 1985).

Limitations in the extrapolation of carbon and mortality conversions globally.—The assumption of a constant mortality rate at a limiting size (Smith 1972) in our conversion from standing stocks to production rates represents a “steady state.” This means that the “observed behavior” of the system (in this case the turnover rate applied), will remain unchanged over time. This is an assumption we make, avoiding the inclusion of data from mass mortality events representing a “non-steady state” system (e.g., Lessios et al. 1984a, b). It is not the purpose of this paper to assess the contribution of mass mortality events to the CaCO_3 inventories, but they certainly merit further characterization and scientific study.

In the extrapolation of carbon data from our model species, we assumed that their biogeochemical composition was similar across species and latitudes, and this is supported by data comparing the Antarctic with temperate and tropical regions (McClintock and Pearse 1987). Additionally, we compiled literature data of percentage dry mass as CaCO_3 in echinoderm skeletons for all latitudes and oceans (data in Vinogradov 1953). We found the following means and standard deviations: $85.61\% \pm 4.14\%$ CaCO_3 in asteroids ($n = 26$ species), $87.52\% \pm 4.24\%$ CaCO_3 in echinoids ($n = 17$ species), $86.90\% \pm 3.41\%$ CaCO_3 in ophiuroids ($n = 18$ species), and $87.24\% \pm 1.63\%$ CaCO_3 in crinoids ($n = 22$ species). This consistence among species is a major finding, since we may not need to sample many species globally to build up a global CaCO_3 budget. The differences across species, at least in the inorganic carbon fraction, are minor. These data support our limited use of echinoderm samples as model organisms in this data set.

Data analyses.—All statistical analyses were performed in Minitab 14.0 (Minitab, State College, Pennsylvania, USA). Data were normally distributed after a log transformation. A general linear model (GLM) was run to compare the carbon content differences across classes and species due to an unbalanced design (the model is $y = X\beta + \varepsilon$, $X_i\beta_i + \varepsilon_i$, where y is carbon, X is class, X_i is species, β is the vector of coefficients, and ε is the vector of residuals). The same GLM type was used to assess the carbon standing stock in the four oceans (Atlantic Ocean + Mediterranean Sea, Pacific Ocean, Southern Ocean, and Arctic Ocean) and among the five echinoderm classes (where X is ocean, X_i

is class). Post hoc analyses (Tukey test) were subsequently performed to assess further differences. All mapping work was carried out in ArcGIS 9.2 (ESRI, Redlands, California, USA), and graphics plotted in SigmaPlot 9.0 (Systat, Chicago, Illinois, USA).

Calcite saturation (Ω -Ca) depth calculations and echinoderms global distribution

Global calcite saturation (Ω -Ca) data were highlighted in areas extensively populated by echinoderms, as it is these populations that will be adversely affected first by the predicted shoaling in saturation depth. Ω -Ca data were calculated from the GLODAP bottle database (*available online*)⁶ (also see Appendix: Fig. A1; Key et al. 2004, Sabine et al. 2005). The Ω -Ca calculations were done with the software CO2SYS (CO₂ System Calculations; Lewis and Wallace 1998, Pierrot et al. 2006). The calculations used the dissociation constants from Mehrbach et al. (1973) refitted by Dickson and Millero (1987), KHSO_4 from Dickson (1990), and the input parameters were dissolved inorganic carbon (DIC), titration alkalinity (TA), temperature, salinity, pressure, silicate, and phosphate in situ. To construct a global map of the calcite saturation depth (Ω -Ca = 1) at depth, all the data were gridded in the software Surfer (Golden Software, Golden, Colorado, USA) inside a polygon to ensure it would not grid on land (minimum curvature method, with a grid size of $2^\circ \times 2^\circ$). Ω -Ca data were also calculated from the GLODAP carbon database and from cruise Niskin bottle data (Arctic Ocean) at specific locations and depths where echinoderm data were also available. There are limited data from the Arctic Ocean, and the Ω -Ca values presented here do not represent a comprehensive and detailed representation of the Arctic Ocean.

Data to assess the echinoderms global distribution and put it in perspective with the present saturation horizons were compiled from the Census of Marine Life (*available online*),⁷ the Ocean Biogeographic Information System (*available online*),⁸ and published literature. The databases were extensively explored and data were compiled individually for the five echinoderm classes (see “Other data” in Fig. 2). This data set provides a limited understanding of the distribution of the echinoderms since many species are missing (see Pawson 2007, Uthicke et al. 2009 for an update). Moreover, the records are potentially biased toward those locations where more samples have been collected, and places such as the Arctic Ocean, Southern Ocean, and the east Pacific are probably undersampled. Another substantial source of uncertainty and lack of data is the deep waters, where ophiuroids, for example, are known to exist at high densities (Blaber et al. 1987, Metaxas and Giffin 2004).

⁶ http://cdiac.ornl.gov/oceans/glodap/Glodap_home.htm

⁷ <http://www.coml.org/>

⁸ <http://www.iobis.org/>

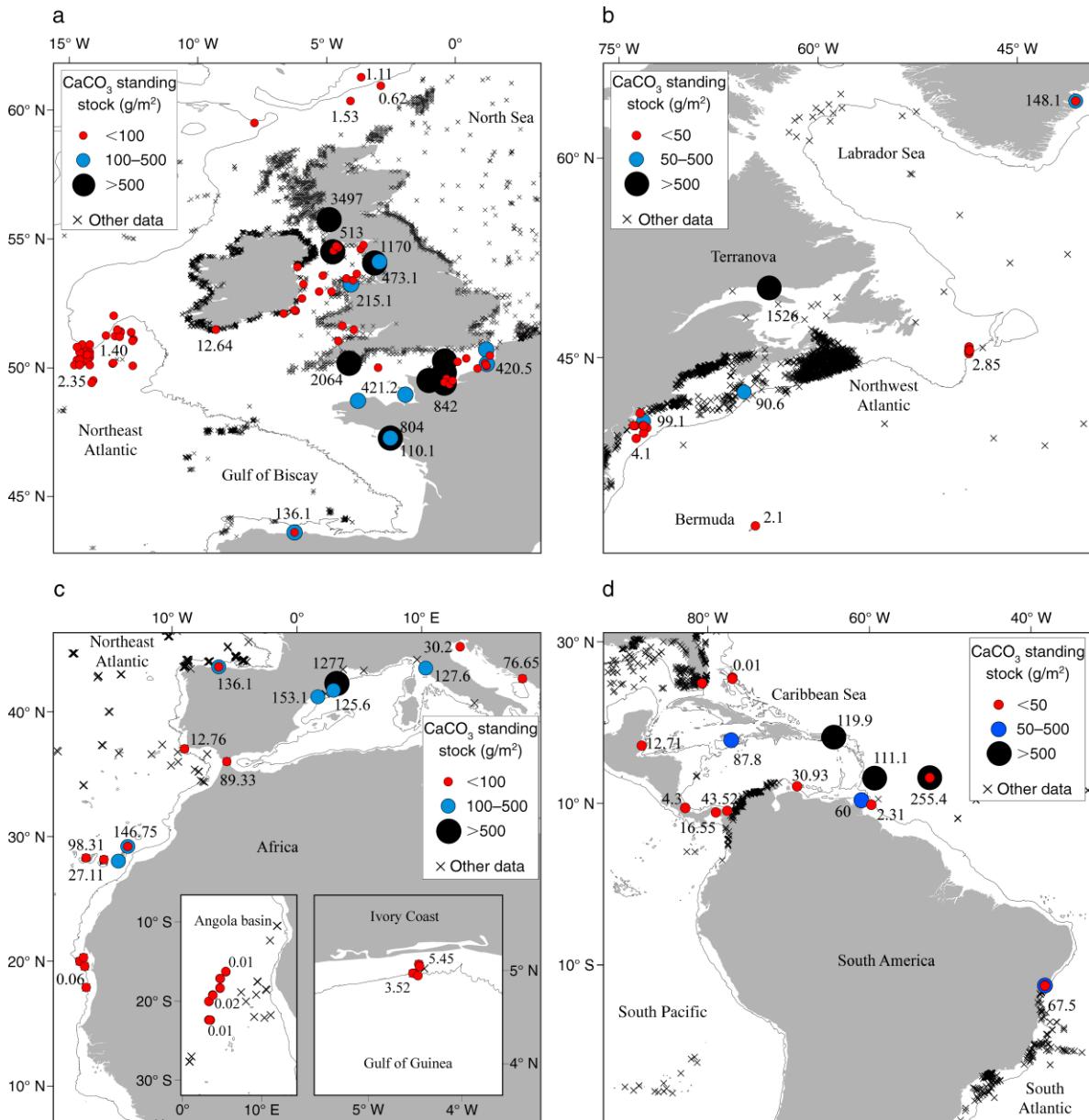


FIG. 2. Geographical distribution of the calculated CaCO_3 standing stock from echinoderms: (a) northeast Atlantic, (b) northwest Atlantic, (c) east-equatorial Atlantic and Mediterranean Sea, (d) west-equatorial Atlantic and south Atlantic, (e) north Pacific, (f) west and south Pacific, (g) Southern Ocean, and (h) Arctic Ocean. Colored symbols indicate the estimated CaCO_3 standing stock, and black crosses indicate the sites where echinoderms have been recorded. The gray bathymetric line represents the 1000-m break.

RESULTS

Echinoderm carbon measurements

The organic (OC) and inorganic carbon (IC) (including CaCO_3) content as a function of the dry mass was significantly different among classes (OC, $F_{4,54} = 52.01$, $P < 0.01$; IC/ CaCO_3 , $F_{4,54} = 265.59$, $P < 0.01$), and among species within the same class (OC, $F_{3,54} = 10.17$, $P < 0.01$; IC/ CaCO_3 , $F_{3,54} = 3.64$, $P < 0.05$; Table 3). The maximum difference in OC between any two classes

was 22% (holothurian–echinoid), while between species within the same class it was 9% (asteroids). For inorganic carbon (IC), the maximum difference between any two classes achieved was 10% (83% of CaCO_3 ; echinoid–holothurian), and among species it was 3% (23% of CaCO_3 ; echinoids). The percentage of OC was highest in holothurians ($27.44\% \pm 2.01\%$; all data shown are mean \pm SD), followed by asteroids ($18.75\% \pm 5.37\%$), while for CaCO_3 , echinoids ($86.83\% \pm 1.42\%$), ophiuroids ($77.91\% \pm 1.24\%$), and crinoids ($72.86\% \pm$

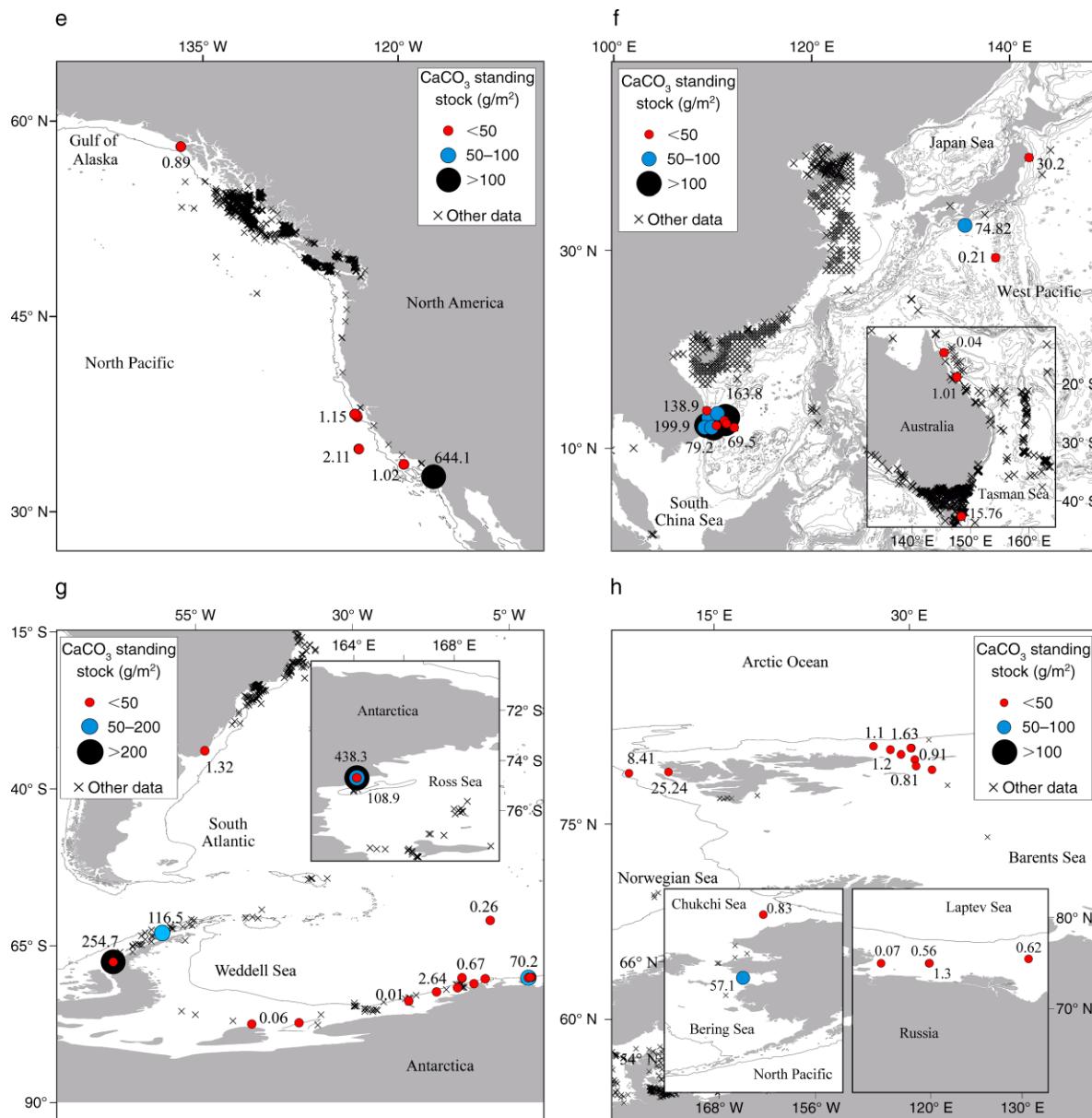


FIG. 2. Continued.

1.36%) had the highest proportions. Inorganic to organic carbon ratios (IC/OC) varied from <1 in asteroids to >1.5 in echinoids and ophiuroids.

Global patterns of echinoderm carbon

Standing stocks per unit area and global production rates.—The calculated echinoderm global CaCO₃ standing stocks and production rates were strongly differentiated and “patched” in the four oceans studied (Atlantic Ocean + Mediterranean Sea, Pacific Ocean, Southern Ocean, and Arctic Ocean). There were significant differences among oceans ($F_{3,515} = 17.78$, $P < 0.01$) and classes ($F_{4,515} = 15.85$, $P < 0.01$). The post hoc analysis (Tukey test) revealed the following

underlying differences in the CaCO₃ standing stocks and production rates at $P < 0.05$: (1) Atlantic Ocean, significant differences among all combinations of classes; (2) Pacific Ocean, significant differences among the Asterozoidea, Echinozoidea, and Ophiurozoidea, among the Echinozoidea, Ophiurozoidea, and Holothurozoidea, and between Echinozoidea and Crinozoidea; (3) Southern Ocean, only significant differences between the Asterozoidea and the other classes; (4) Arctic Ocean, only significant differences between the Asterozoidea and the Crinozoidea.

The global averaged standing stock of carbon derived from echinoderms at all areas is partitioned as follows: 7.97 g C/m² organic carbon, 7.60 g C/m² inorganic

TABLE 4. Echinoderm standing stock of organic carbon (OC), inorganic carbon (IC), and CaCO₃, given as means, with minimum and maximum values calculated globally for all areas (for class) and for the shelf, slope, and abyssal areas (for depth); calculated CaCO₃ production rates based on the conversion data in Smith (1972) are also included.

Category	n§	Carbon standing stock (g C/m ²)†				CaCO ₃ Mean
		OC		IC		
		Mean	Range	Mean	Range	
Class						
Asteroidea	170	9.68	9.65 × 10 ⁻⁷ -630.88	3.10	4.71 × 10 ⁻⁷ -196.95	25.82
Echinoidea	132	6.28	2.48 × 10 ⁻⁶ -152.44	8.01	3.72 × 10 ⁻⁶ -181.23	66.72
Ophiuroidea	156	1.87	5.29 × 10 ⁻⁵ -29.24	15.29	1.23 × 10 ⁻⁶ -510.15	127.36
Holothuroidea	41	10.34	7.89 × 10 ⁻⁷ -326.50	0.02	8.02 × 10 ⁻⁷ -0.44	0.16
Crinoidea	24	0.16	8.48 × 10 ⁻⁸ -3.39	0.17	8.74 × 10 ⁻⁸ -3.50	1.41
Mean†	523	7.97	8.43 × 10 ⁻⁸ -630.88	7.60	8.74 × 10 ⁻⁸ -510.15	63.34
Depth						
Shelf (0-200 m)	164	21.77	9.65 × 10 ⁻⁷ -630.88	22.31	4.71 × 10 ⁻⁷ -510.15	184.77
Slope (200-2000 m)	180	2.23	8.48 × 10 ⁻⁸ -98.70	0.90	8.74 × 10 ⁻⁸ -28.35	7.51
Abyssal (>2000 m)	78	0.023	2.48 × 10 ⁻⁶ -0.75	0.015	8.74 × 10 ⁻⁸ -28.35	0.12

† Data calculated as global means of the five classes from the 523 sites at all depths. The mean is not from data of the five classes directly from the table.

‡ Conversion made from standing stocks with data from Smith (1972), which includes a turnover factor (see *Materials and methods*).

§ Number of locations (data compiled from the literature).

¶ Calculated with 3.24 g C·m⁻²·yr⁻¹ as inorganic carbon.

Calculated with 9.35 g C·m⁻²·yr⁻¹ as inorganic carbon.

|| Calculated with 0.24 g C·m⁻²·yr⁻¹ as inorganic carbon.

†† Calculated with 0.006 g C·m⁻²·yr⁻¹ as inorganic carbon.

carbon, and 63.34 g CaCO₃/m² (Table 4). Bathymetrically, the major contribution originates in the shelf, with values for all carbon compartments over an order of magnitude higher than in the slope and the abyssal depths (Table 4). The major contribution of organic carbon is from holothurians (10.34 g C/m²) and asteroids (9.68 g C/m²), while ophiuroids (127.36 g CaCO₃/m²) and echinoids (66.72 g CaCO₃/m²) contribute the most CaCO₃ (Table 4). In terms of the annual global CaCO₃ production in all areas based on the field data turnover rates, echinoderms produce 27.01 g CaCO₃·m⁻²·yr⁻¹ on average (3.24 g C·m⁻²·yr⁻¹ as inorganic carbon), with echinoids (66.72 g CaCO₃·m⁻²·yr⁻¹) and ophiuroids (25.47 g CaCO₃·m⁻²·yr⁻¹) producing the most (Table 4). The CaCO₃ production in the shelves is 77.91 g CaCO₃·m⁻²·yr⁻¹ (9.35 g C·m⁻²·yr⁻¹ as inorganic carbon), which is over an order of magnitude higher than the production in the slopes and abyssal depths of 2.05 and 0.056 g CaCO₃·m⁻²·yr⁻¹ respectively (0.24 and 0.006 g C·m⁻²·yr⁻¹ as inorganic carbon respectively; Table 4).

Using these data along with the global figures of the areas occupied by the shelves (~10 × 10¹² m²), slopes (~32 × 10¹² m²), and the abyssal depths (~290 × 10¹² m²), the echinoderms CaCO₃ standing stock translates into ~1.84 × 10¹⁵ g CaCO₃, ~0.24 × 10¹⁵ g CaCO₃, and 0.037 g CaCO₃, respectively (0.22 × 10¹⁵, 0.028 × 10¹⁵, and 0.0044 g C as inorganic carbon, respectively). The total is 2.11 × 10¹⁵ g CaCO₃ (0.25 × 10¹⁵ g C as inorganic carbon). On the production side, echinoderms account for ~0.78 × 10¹⁵ g CaCO₃/yr (0.093 × 10¹⁵ g C/yr as inorganic carbon) from the shelves, ~0.065 × 10¹⁵ g CaCO₃/yr (0.0078 × 10¹⁵ g C/yr as inorganic carbon)

from the slopes, and ~0.016 × 10¹⁵ g CaCO₃/yr (0.0019 × 10¹⁵ g C/yr as inorganic carbon) from the abyssal depths (Table 5). This translates into a final global figure of ~0.861 × 10¹⁵ g CaCO₃/yr (0.102 × 10¹⁵ g C/yr as inorganic carbon) for the shelves, slopes, and abyssal depths together (Table 5).

Geographical distribution of the CaCO₃ standing stock.—The available data for calculation of CaCO₃ standing stocks were patchily distributed in all areas studied, limiting a detailed characterization of the carbon budget. This patchiness can be observed in detail in Fig. 2. In the northeast Atlantic (Fig. 2a), CaCO₃ produced by echinoderms attained values >2000 g/m², especially in the Irish Sea and the English Channel. Ophiuroids (*Ophiothrix fragilis*, *Ophiocomina nigra*, *Ophiopholis aculeata*), asteroids (*Asterias rubens*, *Hymenaster* spp., *Astropecten irregularis*), and echinoids (*Psammechinus miliaris*, *Echinus* spp.) accounted for the majority of the calculated CaCO₃ stocks. The carbonate stock in the well-sampled Porcupine Seabight (1000–1400 m depth) deep areas was relatively low compared with that in shallow water. Other areas around Ireland and Scotland, as well as the North Sea, revealed a conspicuous presence of echinoderms, which may well bear substantial CaCO₃ stocks. In the northwest Atlantic (Fig. 2b), although limited data were available, a substantial contribution was observed, between 100 and >1000 g CaCO₃/m², mainly by ophiuroids (*Ophiopholis aculeata*, *Ophiacantha abyssicola*, *Ophiomusium lymani*). Areas such as the New England continental slope are well known to harbor high biomass of echinoderms. In the east and equatorial Atlantic (Fig.

TABLE 4. Extended.

Carbon standing stock (g C/m ²)†	Production (g CaCO ₃ ·m ⁻² ·yr ⁻¹)‡	
	CaCO ₃	
	Range	Mean
3.92 × 10 ⁻⁶ –1640.59	7.76	1.17 × 10 ⁻⁶ –492.18
3.10 × 10 ⁻⁵ –1509.71	66.72	3.10 × 10 ⁻⁵ –1509.71
1.02 × 10 ⁻⁵ –4249.54	25.47	2.05 × 10 ⁻⁶ –849.91
6.68 × 10 ⁻⁶ –3.66	0.070	2 × 10 ⁻⁶ –1.10
7.28 × 10 ⁻⁷ –29.15	0.42	1.81 × 10 ⁻⁷ –8.74
7.28 × 10 ⁻⁷ –4249.54	27.01¶	2.18 × 10 ⁻⁷ –1509.71
3.92 × 10 ⁻⁶ –4249.57	77.91#	1.17 × 10 ⁻⁶ –1509.71
7.28 × 10 ⁻⁷ –236.21	2.05	2.18 × 10 ⁻⁷ –70.86
6.68 × 10 ⁻⁶ –3.07	0.056††	2 × 10 ⁻⁶ –2.47

2c), very few CaCO₃ values were calculated, and they were mainly derived from the Mauritania slope (<1 g CaCO₃/m²), the Canary Islands (<200 g CaCO₃/m²), the Angola Basin (<1 g CaCO₃/m²), and the Ivory Coast (<10 g CaCO₃/m²). The majority of these data were based on echinoid populations (*Paracentrotus lividus*, *Arbacia lixula*, *Diadema antillarum*). In contrast, the Mediterranean Sea had values >100 g CaCO₃/m² in several areas, entirely due to the echinoid *Paracentrotus lividus* (Fig. 2c). In the west and equatorial Atlantic (Fig. 2d), mainly in areas of the Caribbean Sea, CaCO₃ levels always remained <300 g CaCO₃/m². Echinoids also dominated the CaCO₃ production (*Echinothrix* spp., *Triploneustes* spp., *Diadema antillarum*). Few data were analyzed in the northeast Pacific (Fig. 2e), with values <5 g CaCO₃/m² derived from asteroids (*Henricia* spp.) and ophiuroids (*Amphiura* spp.). CaCO₃ values were >500 g/m² from asteroids (*Pisaster* spp.) and echinoids

TABLE 5. Reassessment of the global CaCO₃ budget with updates of recent organism-level measurements.

Production term	Production estimate (Pg C/yr)	Area (10 ¹² m ²)	Reference
Sources			
Neritic†			
Coral reefs	0.108	0.6	Iglesias-Rodriguez et al. (2002)
Halimeda bioherms	0.02		Iglesias-Rodriguez et al. (2002)
Banks/bays	0.048	0.8	Iglesias-Rodriguez et al. (2002)
Non-carbonate shelves			
Shelves†	0.024–0.120	10	Iglesias-Rodriguez et al. (2002)
Slopes†	0.06	32	Iglesias-Rodriguez et al. (2002)
Pelagic			
Euphotic zone	0.6–1.6 ± 0.3‡	300	Balch et al. (2007)§
Export < 100 m	0.6		Sarmiento et al. (2002)¶
Export < 2000 m	0.4 ± 0.05‡		Honjo et al. (2008)¶
Export from models	0.4–1.8		Moore et al. (2004)
Organism level			
Foraminifera	0.036–0.065	290	Schiebel (2002)#
Fish (pelagic)	0.04–0.11	300	Wilson et al. (2009)
Molluscs (neritic)	0.047	1.8	Chauvaud et al. (2003)††
Pteropods (pelagic)	0.87		Gangstø et al. (2008)
Echinoderms (shelves)	0.093	10	this study‡‡
Echinoderms (slopes)	0.0078	32	this study‡‡
Echinoderms (abyssal)	0.0019	290	this study‡‡
Total	0.96–2.56		
Sinks			
Dissolution (200–1500 m)	1	300	Berelson et al. (2007)
Dissolution in the seafloor (>2000 m)	0.4 ± 0.03‡	300	Berelson et al. (2007)
Buried in sediments	0.10	300	Catubig et al. (1998)
Total	1.50		Catubig et al. (1998)

Notes: Data have been summarized from other studies, apart from the data from this study. All values are converted to Pg C/yr as inorganic carbon (1 Pg = Gt = 10¹⁵ g). The total in sources is an approximation from the sum of what we know. It is a range, since all studies have their own error, and giving a figure as such is impossible. The total in sinks comes only from the work in the water column, and it is the sum of the different figures. Blank cells indicate that data are not available.

† Original data in Milliman (1993).

‡ Range or mean ± SE.

§ Satellite production estimation.

¶ Sediment trap flux data.

Multinet and sediment trap flux data at 500 m. No production rate data.

|| Model output.

†† Global extrapolation based on data from three stations off California over a period of 7 years.

‡‡ 0.102 Pg C/yr as a global figure for all areas. Global extrapolation is based on data from 523 stations.

(*Strongylocentrotus franciscanus*). The west and south Pacific areas (Fig. 2f), especially the Indo-Pacific, were extremely undersampled, and the only calculations were available from the south China Sea. CaCO_3 standing stock values remained $<200 \text{ g/m}^2$ with a well-mixed suite of species from the five classes, mainly dominated by echinoids (*Diadema* spp., *Echinometra lucunter*, *Echinothrix* spp.). In the vicinity of the Philippine Sea, the echinoid *Anthocidaris crassispina* accounted for $>70 \text{ g CaCO}_3/\text{m}^2$ while the ophiuroid *Ophiura sarsii* accounted for $30 \text{ g CaCO}_3/\text{m}^2$ near the Tsugaru Strait (Japan Sea). The Australian, Tasman, and New Zealand coasts are well known to shelter high echinoderm biomass, but were also undersampled, with estimations $<20 \text{ g CaCO}_3/\text{m}^2$ attributed mainly to the ophiuroid *Ophiacantha fidelis*. The Southern Ocean (parts of the south Atlantic, Weddell Sea, and Ross Sea; Fig. 2g) were reasonably sampled, with CaCO_3 calculations $<500 \text{ g/m}^2$. The main contributors were asteroids (*Odontaster validus*), echinoids (*Sterechinus neumayeri*), and ophiuroids (*Ophionotus victoriae*, *Ophiurolepis gelida*). Lastly, in the Arctic Ocean data were scarce (Fig. 2h), and calculations remained $<60 \text{ g CaCO}_3/\text{m}^2$, with the echinoid *Strongylocentrotus pallidus* and a suite of asteroids (*Hymenaster* spp.) and ophiuroids (*Ophiacantha* spp., *Ophiocten* spp., *Ophiura* spp.) dominating the CaCO_3 stock.

Bathymetric trends in the CaCO_3 standing stock according to ocean basin.—The CaCO_3 standing stock of echinoderms is inversely related to depth in all oceans, with differences of several orders of magnitude in the gradient of this regression according to latitude (Fig. 3). Within the same ocean there were also marked contrasts; in the Atlantic, the averaged CaCO_3 standing stock at temperate latitudes attained $127.43 \text{ g CaCO}_3/\text{m}^2$, compared to $13.96 \text{ g CaCO}_3/\text{m}^2$ in the tropical regions (Fig. 3). In the Pacific, the situation was reversed with the tropical latitudes supporting roughly $70 \text{ g CaCO}_3/\text{m}^2$ and the temperate ones $16.75 \text{ g CaCO}_3/\text{m}^2$. The Southern Ocean presented on average a higher standing stock than the Arctic Ocean at any one depth, with a mean of $32.21 \text{ g CaCO}_3/\text{m}^2$ compared to $2.65 \text{ g CaCO}_3/\text{m}^2$ (Fig. 3). The standing stock calculations in any ocean revealed much less variability in the tropics than at higher latitude. The standard deviation of all the Atlantic temperate data was $\pm 471 \text{ g CaCO}_3/\text{m}^2$ while in the tropics it was $\pm 34.77 \text{ g/m}^2$, compared to ± 89.15 (temperate) and $\pm 66.02 \text{ g/m}^2$ (tropical) in the Pacific. More than 80% of the substantial CaCO_3 stocks ($>10 \text{ g CaCO}_3/\text{m}^2$) were found in waters shallower than 800 m, and especially from 0 to 500 m (Fig. 3). This coincided with the neritic, shelf, and slope areas in most regions. The deep-sea areas sampled presented a low CaCO_3 standing stock per unit area, progressively decreasing down to 4000–5000 m. However, the area covered by the benthic systems at bathyal and abyssal depths cannot be ignored on a global scale. Moreover, data originating deeper than 2000 m only accounted for 19% of the data

set, while $>60\%$ of the data were recorded shallower than 500 m.

Global Ω -Ca saturation horizons in echinoderm-rich areas

The global distribution of adult echinoderms and their potential carbon contribution based on the available data reveals clear trends (Fig. 4). Continental margins are the areas most populated, with thousands of records. Especially the west and northwest Atlantic, east Atlantic, east and west Pacific, and the south Pacific (New Zealand, Tasman Sea) presented the majority of the echinoderm records (Fig. 4). Deep-sea data were scarce, and therefore our understanding of their contribution to the global carbon budget is limited. The deep-sea echinoderm's biogeography and contribution to the CaCO_3 inventory is even more complicated to assess with the knowledge of very low Ω -Ca saturation values deeper than 4000 and 1000 m in the Atlantic and Pacific Ocean, respectively (see graphs in Fig. 4): The depth where the Ω -Ca = 1.0 (saturation state) gets closer to the surface from the Atlantic, to the Indian, and to the Pacific Ocean, approaching the surface in the north Pacific (see Feely et al. 2004 for details). The situation in enclosed basins such as the Mediterranean Sea is different, and undersaturation is not even achieved at the seabed $<2000 \text{ m}$ (see Millero et al. 1979).

The in situ Ω -Ca saturation horizons where adult echinoderm populations have been recorded varied depending on latitude and depth (see graphs in Fig. 4). From 0 to 300 m, the mean Ω -Ca saturation in the Atlantic (5.01) and the Pacific (4.79) are similar. Deeper than that, the mean saturation in the Atlantic is higher (2.65 between 300 and 1000 m, and 1.84 between 1000 and 2500 m) in comparison with the Pacific (2.03 between 300 to 1000 m, and 0.94 between 1000 and 2500 m). In the northwest Pacific, Ω -Ca values are relatively close to undersaturation (1.66) at 250 m in some areas (see graph in Fig. 4), while beyond 1000 m they are already undersaturated. Undersaturation in the north and south Atlantic only occurs deeper than 4000 m. The Southern Ocean data reveal no undersaturation down to 2000 m (see graph in Fig. 4), but there are values near the Ω -Ca = 1 threshold between 300 m (Ω -Ca = 1.88) and 2000 m (Ω -Ca = 1.24). The scarce data from the Arctic make it difficult to assess the situation there, but near 600 m Ω -Ca is still 2.42 (see Jutterström and Anderson 2005 for details).

DISCUSSION

CaCO₃ standing stock patchiness

Data presented here show patchiness in echinoderm distribution at large and small scales depending on the species and the population sampled, in agreement with findings by other authors (e.g., Summers and Nybakken 2000). Global data showed high variability in echinoderm density, with dense aggregations occurring in some places, while being almost nonexistent at others. This

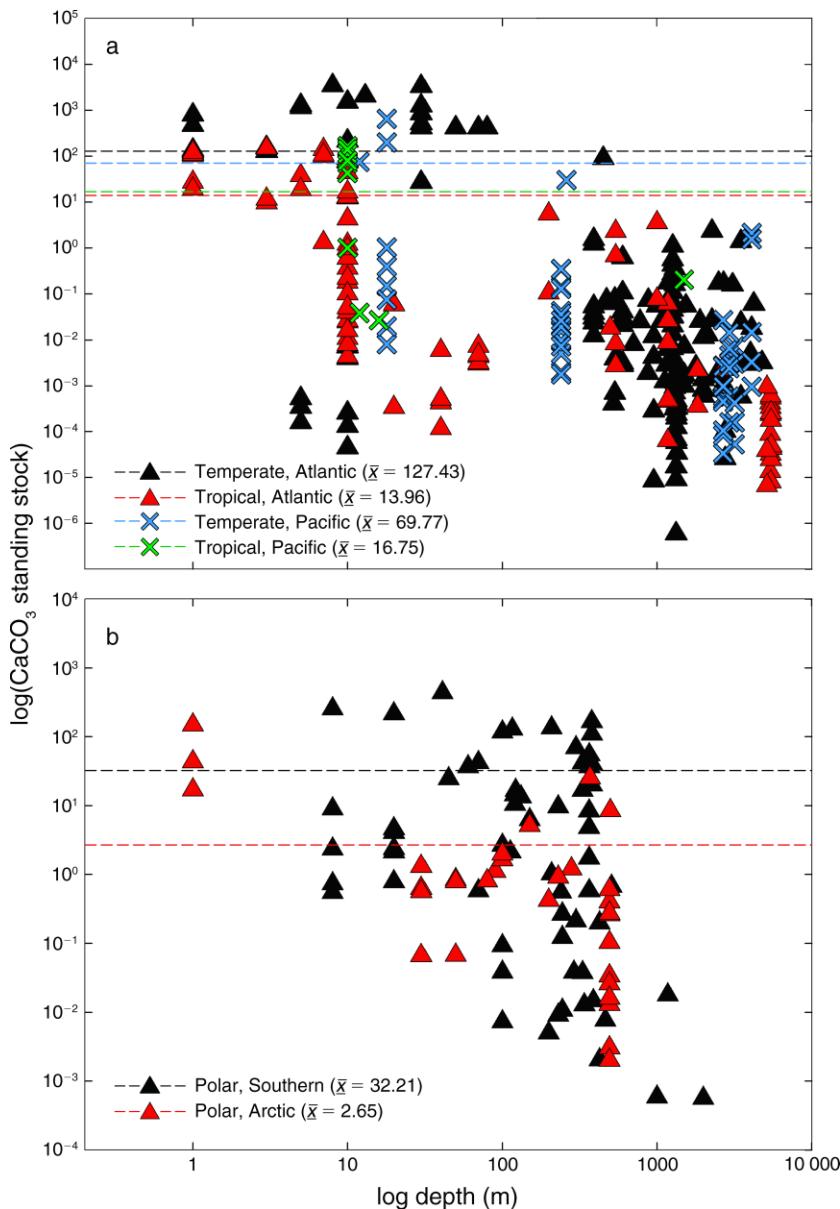


FIG. 3. Log of echinoderm global CaCO_3 standing stock (originally measured as g C/m^2) in relation to log of depth (originally measured in meters) for temperate ($30-64^\circ$ N, $30-64^\circ$ S), tropical (30° N– 30° S), and polar latitudes ($>64^\circ$ N, $>64^\circ$ S) in (a) the Atlantic ($n = 245$) and Pacific Oceans ($n = 68$) and (b) the Southern ($n = 64$) and Arctic Oceans ($n = 29$). A log scale is used to visualize the data. Mean CaCO_3 standing stocks for each latitudinal range (irrespective of depth) are also included as dashed lines.

partitions the echinoderms CaCO_3 inventory in an immense mosaic of “hot spots” with a clear trend of decrease in carbon per unit area with depth, and a slight decrease toward the low latitudes (see Fig. 3). In this study, the bathymetric trends created spatial patchiness in the CaCO_3 stocks observed. Howell et al. (2002) showed that the maximum abundance of asteroids over large depth gradients is observed only in ranges of 200–300 m. The same is recorded for ophiuroids (and for all echinoderms), since their bathymetric distribution shows a dependence on food (Haedrich et al. 1980), oxygen

(Summers and Nybakken 2000), seabed properties (Mayer and Piepenburg 1996), and temperature (Garcia et al. 2002). Recently, Cartes et al. (2009) provided information on bathymetric patchiness and hot spots of biomass for echinoderms in the Mediterranean Sea. These data support our conclusion of large hot spots of CaCO_3 globally following depth and latitudinal gradients.

The highest CaCO_3 contribution beyond neritic waters is from ophiuroids, which are known to dominate various habitats in the shelves, slopes, and deep sea (Smith and Hamilton 1983, Blaber et al. 1987, Shin and

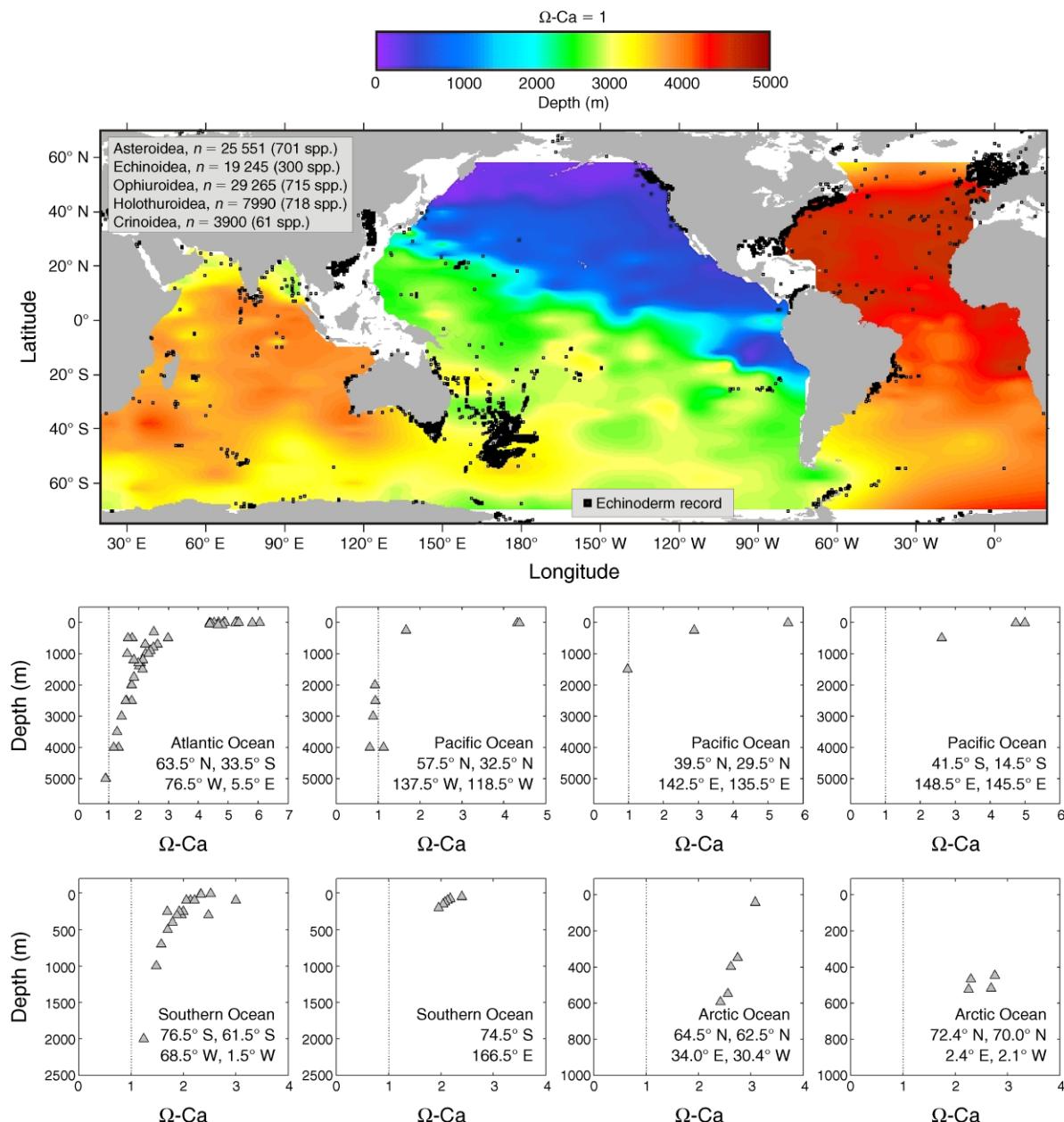


FIG. 4. Global distribution of the calcite saturation depth ($\Omega = 1$). When the degree of saturation, Ω , is >1 , seawater is supersaturated. With calcite, seawater is undersaturated with respect to this mineral when Ω -Ca < 1 . Echinoderm global distribution data are overlaid as black squares. Note that the number of species per class is related to the data in the map and not to the present number of species found in sampling (see Pawson [2007] and Uthicke et al. [2009] for an update). Numerical data shown are number of individuals with number of species in parentheses. Also shown are plots of depth against profiles of Ω -Ca at sites where echinoderms were recorded in the database (geographical information presented in graphs). There was only one set of coordinates available for the Southern Ocean.

Koh 1993). They have been especially ascribed to the upper continental slope (Marshall 1979; see Fig. 5 for a visual illustration of high densities of ophiuroids in different areas). This can be seen from the data (Fig. 3), where the maximum CaCO_3 standing stocks per unit area occurred at depths where ophiuroids are known to exist in dense aggregations (e.g., Metaxas and Giffin

2004). In the Atlantic Ocean the maximum standing stock recorded from ophiuroids was $>3000 \text{ g CaCO}_3/\text{m}^2$. However, in the Pacific and the Southern Ocean, echinoids accounted for the maximum standing stocks ($<700 \text{ g CaCO}_3/\text{m}^2$), especially in the neritic areas. High ophiuroid densities occur in shelves and slopes from 200 to >2000 individuals/ m^2 (Warner 1971, Blaber et al.

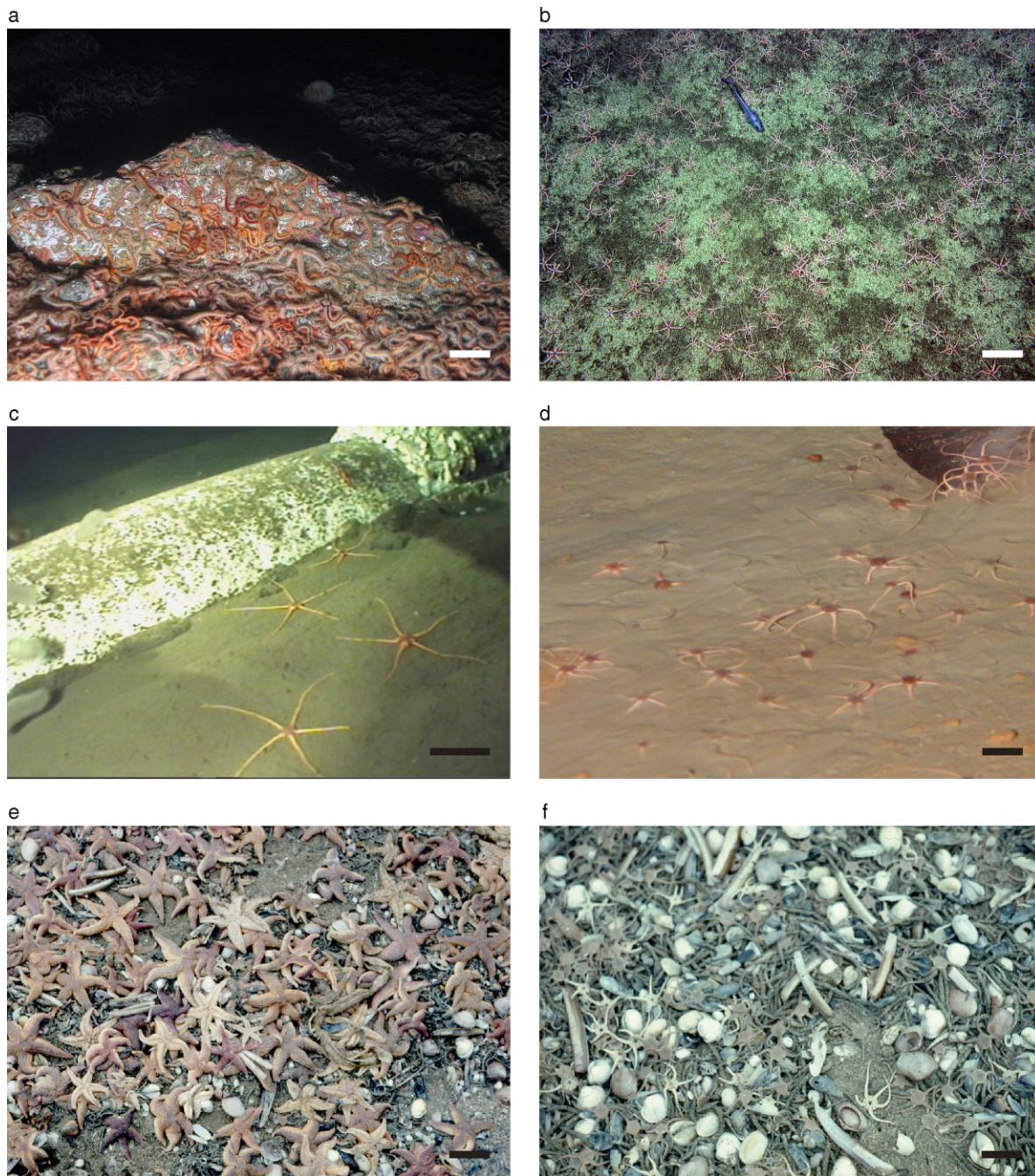


FIG. 5. Aggregations of living and freshly deposited echinoderms on shelves and slopes. (a) Dense *Ophiothrix fragilis* bed on the shelf at 50 m depth off the Shetland Islands (north of Scotland; copyright © D. O. B. Jones, SERPENT project), (b) dense ophiuroids bed on the slope at 613 m depth off Peru from the research vessel *Meteor*, cruise 77-1 (IFM-GEOMAR department SFB754; T. Mosch, unpublished data), (c) ophiuroids (ophiolepadidae) on the slope at 935 m depth off Ivory Coast (photo credit: M. Lebrato and D. O. B. Jones), and (d) *Ophiacantha bidentata* aggregation on the slope at 1400 m depth in the Norwegian Sea (copyright © A. Gates, SERPENT project). (e) Freshly deposited carcasses from the starfish *Asterias rubens* and (f) from an ophiuroid in the Normandy-Boulonnais coasts (northwest France, east Atlantic Ocean); the carcasses were starting to decompose (copyright © I. Harding, National Oceanography Centre, University of Southampton). Scale bars are 200 mm in all cases.

1987), at times covering >60% of the seabed (Blaber et al. 1987; see Metaxas and Giffin [2004] for a detailed discussion of high density areas; Fig. 5). In shallow waters <100 m depth, their distribution is very patchy,

attaining densities between 100 and 1000 individuals/m² at times (see Metaxas and Giffin 2004) but covering <30% of the seabed (Warner 1971; see Fig. 5). In sublittoral shallow waters they occur at much lower

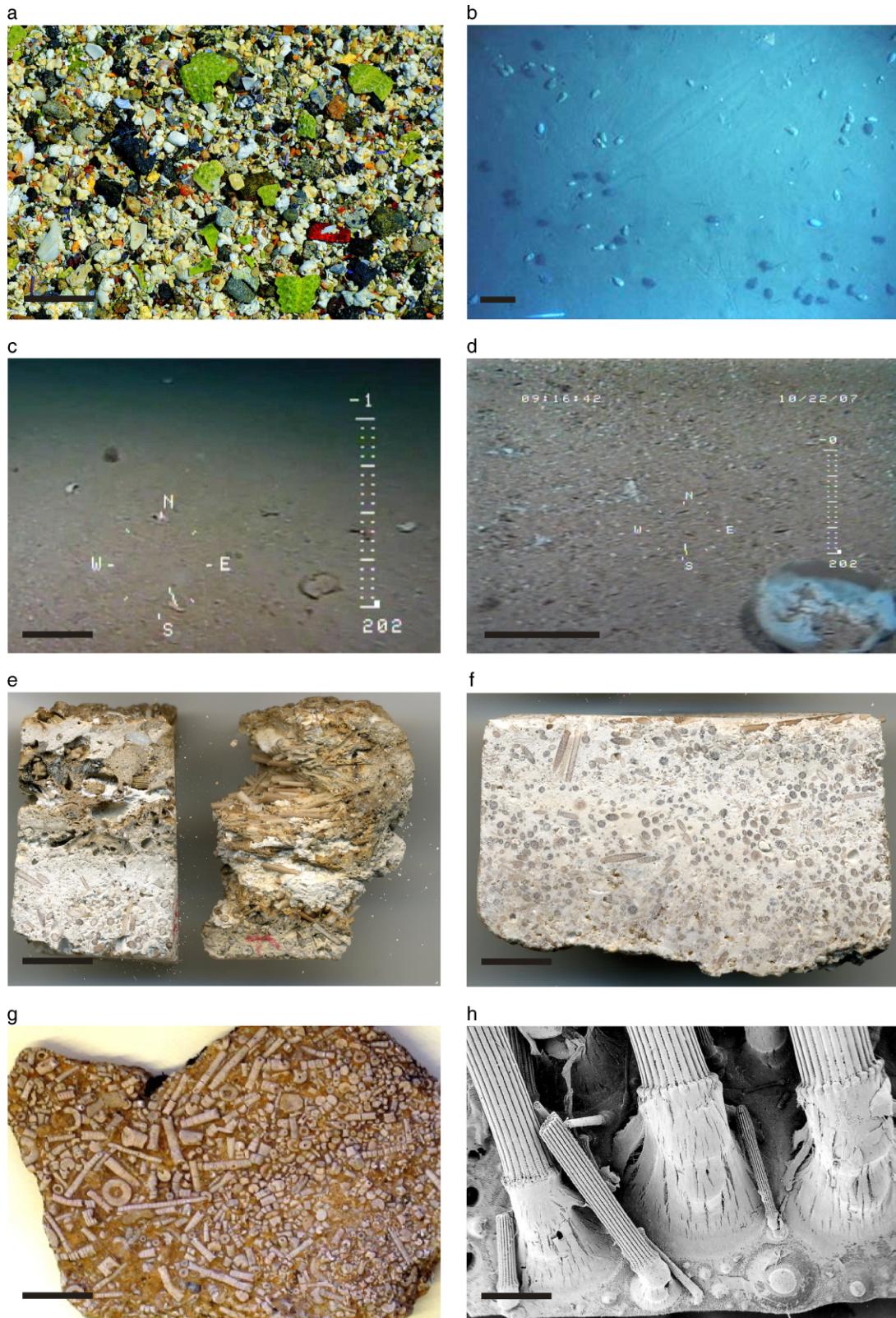


FIG. 6. Echinoderm remains in the present oceans and in the geological record. (a) “Echinoderm sand” and particles (greenish color) along with other shelf calcifier remains visually surveyed in Lanzarote Island (Canary Islands, east Atlantic Ocean; 29° N, 13° W) (photo credit: M. Lebrato). The echinoderm remains dominated (visually) all the areas surveyed both on the top layer and in

densities (Hendler and Meyer 1982). Other echinoderms such as echinoids populate at much higher densities the neritic areas (e.g., Turon et al. 1995). However, in Antarctic regions, echinoids also populate the shelf and the slope in dense aggregations (Brey and Gutt 1991, David et al. 2005). Therefore, as a general rule with exceptions in the low latitudes, ophiuroids account for the majority of the shelf and slope CaCO₃ production, while echinoids do so in the shallow littoral and sublittoral areas. Yet, at finer scales (regional and especially local) these trends may change and rely on factors such as seabed substrate or hydrography (see Cartes et al. 2009). Cartes et al. (2009) show that at regional scales, such as in the western Mediterranean Sea, crinoids and holothurians can dominate the deep shelf and the shelf-slope break with densities up to 15 individuals/m² (Péres 1985). In the deep Mediterranean, holothurians and echinoids dominate the biomass between 400 and 2000 m, which translates into enhanced local hot spots of CaCO₃. In consequence, the trends in the CaCO₃ standing stocks diversify and get more complex at fine scales.

Our global CaCO₃ standing stock data of echinoderms decreased with depth, which is consistent with observations in most Arctic (e.g., Piepenburg et al. 2001), Antarctic (e.g., Jones et al. 2007), and subantarctic studies (e.g., Arntz et al. 1994, Thatje and Mutschke 1999) and is most likely related to reductions in availability of organic matter to the benthos with depth (Lampitt et al. 2001). In areas such as the Mediterranean Sea, echinoderm productivity and CaCO₃ hot spots are highly dependent on the availability of organic matter from canyons (Cartes et al. 2009). Energy availability in deep-sea benthic habitats and thus the possibility for echinoderms to establish significant CaCO₃ hot spots is positively correlated with (1) sediment community respiration (Berelson et al. 1997), (2) the rate of organic carbon burial within the sediment (Jahnke 1996), (3) benthic biomass and abundance (Cosson et al. 1997), and (4) the overlying primary productivity (Lampitt and Antia 1997).

The differences observed among the temperate, tropical, and polar regions in terms of the echinoderms

CaCO₃ standing stock may be attributable to highly seasonal pulses of primary production at low latitudes (Picken 1985). The “quality” rather than the “quantity” of food reaching the seabed may also explain at fine and broad scales the discontinuities and peaks of echinoderms biomass and CaCO₃ globally (Billett and Hansen 1982, Hudson et al. 2004). Moreover, latitudinal trends are highly dependent on the organism-level carbon values measured, and at present we do not have any data from species either in the Arctic or the Antarctic. Watson et al. (2008) showed that the shell of an Antarctic echinoid (*Sterechinus neumayeri*) was 15% thinner than a temperate species (*Psammechinus miliaris*). We hypothesize that this could be a consequence of the mineral composition (Vinogradov 1953) and the lower mineral saturation states of the waters (Orr et al. 2005). Echinoderms will need to allocate more energy to calcify, and this will explain the occurrence of thinner shells and potentially less carbon. If this is a common feature in all echinoderms, then the carbon they can produce as organisms will be reduced at the high latitudes. In turn, this could be compensated by increasing the population density and biomass.

Processes in the sediments and in the geological record

The fate of the echinoderms CaCO₃ at the seabed.—The high productivity of echinoderms in terms of CaCO₃ and their carbon standing stocks eventually result in their downward flux at/to the seafloor through mortality. Sources of echinoderm mortality (see Rees and Dare 1993) that could result in a flux of CaCO₃ include burial and wash out resulting from wave energy (Anger et al. 1977) and storm events (see Fig. 6a, b), exposure to unusual temperatures and desiccation (Schafer 1972, Verling et al. 2005), predation (Menge 1979, Cartes 1994), prolonged hypoxia due to eutrophication and collapse of algal blooms (Rosenberg and Loo 1988), trawling (Bergman et al. 1990), natural mortality (Scheibling and Stephenson 1984; see Fig. 6d for mortality, e.g., in the deep sea), and disease (Bauer and Young 2000). As a general rule, mortality rates increase with increasing latitude (Bullock 1955). This has major implications for the carbon inventories in the

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the sediment underneath; the scale bar is 30 mm. (b) Echinoids living at the seabed (dark) and freshly deposited carcasses (bright) at >1000 m depth off west Africa; the scale bar is 300 mm (copyright © SERPENT project). (c, d) Echinoid remains at 203 m depth in the Ibiza Channel (Mediterranean Sea) (38.65° N, 0.94° E) from the EUROLEON cruise (numbered REN2002-11216E; copyright © Laia Beni-Casadella and Miquel Canals, GRC-GM [Grup de Recerca Consolidat en Geociències Marines, Universitat de Barcelona], HERMES project); the scale bar is 150 mm. (e, f) Echinoderm remains at 717 m depth in sediment core sections (numbered JR31-BGS9; copyright © C. J. MacLeod) from the Atlantis Bank massif adjacent to the Atlantis II fracture zone (southwest Indian Ocean; 32.6° S, 57.3° E) (for details, see MacLeod et al. [1998, 2000]). The cores are probably from the Pliocene (2.5–5.3 million years ago), with a matrix of well-lithified micritic calcite. The spines and other remains of echinoids are clearly visible at different sediment depths showing temporal accumulations over thousands of years. The animals probably originated in a much shallower ocean. Scale bars are 8.6 mm. (g) Crinoid fossil remains from the lower Devonian in La Coladilla formation (Cantabrian mountains, northwest Spain; copyright © I. Harding, National Oceanography Centre). Crinoids were the important carbonate producers before the Jurassic. The scale bar is 26 mm. (h) Scanning electron microscope (SEM) image of the decomposition of the echinoid *Echinus esculentus* (copyright © I. Harding, National Oceanography Centre). The organic material (mainly muscle) is decaying. On the front view decaying muscle can be observed (with small fractures) on the attachment to the test tubercles. The same is observed on the back left (between the spines). The scale bar is 1 mm.

polar regions, since echinoderms contribute substantially at the higher latitudes to the CaCO_3 standing stock per unit area (see Figs. 2 and 3). Annual mortality rates of echinoderm populations are species specific and site specific: $<10\%/yr$ (Bluhm et al. 1998, Verling et al. 2005) and $>80\%/yr$ (Lessios et al. 1984a, b, Hunte et al. 1986, Zann et al. 1987). Mortality is also correlated with age, growth, and the limiting size of individuals within the population (see Smith [1972] and references therein for mathematical production models based on mortality). This makes using global data analysis to generate realistic projections of the CaCO_3 production and fluxes from echinoderms based on standing stocks in the global carbon cycle very challenging. The situation gets even more complicated with the occurrence of high mass mortality events in some years where up to 95% of the population perishes (Lessios et al. 1984a, b). This will transfer vast amounts of CaCO_3 to the seafloor. We did not include any of these data into our calculations as already pointed out in *Echinoderms carbon measurements: Echinoderm global carbon data set: Limitations in the extrapolation of carbon and mortality conversions globally*.

Evidence from the subtropical east Atlantic (Canary Islands) and the northeast Atlantic (France) suggests that shallow water echinoderm carcasses are freshly deposited in the intertidal and subtidal environment (Figs. 5e, f, 6a). Eventually, the fragmented CaCO_3 particles form major depositions either on sediments in the vicinity or in sand/boulder beaches (also up the shore far from water after a period of time) forming a denominated "echinoderm sand" (Fig. 6a). In the deep sea, echinoderm mortality is a common natural phenomenon (Fig. 6b–d), with carcasses decomposing in situ, directly incorporating the CaCO_3 into the sediments. Elsewhere, dead echinoderms freshly deposited in high-energy neritic environments may be also retained in the vicinity, rapidly transported offshore in fragments, or remineralized in situ (Verling et al. 2005). After deposition in shallow waters or the deep sea (Fig. 5e, f, Fig. 6b–d), the echinoderm organic material decomposes rapidly (between 4 and 8 days; Glynn 1984), exposing the skeleton, which is usually disarticulated (Weber 1969). The test and spines (in the case of echinoids) are quickly separated by muscle degradation (see Fig. 6h), and the spines are the first to fall off, being deposited in the sediments (Smith 1984). The tests, more rigid and resistant, may be retained for months in situ until buried or disintegrated. A rapid degradation facilitates the retention or the export of their CaCO_3 skeletons into deeper waters, where CaCO_3 is incorporated into sediments (see Moran 1992) or dissolved (Rude and Aller 1991). Echinoderms skeletal carbonate sand and gravel (echinoderm sand) have been described in sediments from coastal margins (Brunskill et al. 2002), along with fragments of foraminifera, benthic algae, bryozoans, and molluscs (see Fig. 6). The carbonate burial rate for echinoderms was estimated to be between 500 and 1700 $\text{g CaCO}_3\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in neritic

zones off Australia (Brunskill et al. 2002). There is sedimentary evidence suggesting the burial of echinoderms carbon at the seabed, especially from sediment cores with recent inorganic carbon skeleton remains of the starfish *Acanthaster planci* (Maxwell 1971). Additional evidence from holothurian spicules and skeletons found in sediment deposits (see Vinogradov 1953) suggest that echinoderm carbon may be quickly incorporated into the sediment, sequestering the CaCO_3 . The most convincing evidence is encountered in sediment cores from the Pliocene (2.5–5.3 million years; C. J. MacLeod, unpublished data) with echinoid deposits over thousands of years (Fig. 6e, f). Moreover, records in rocks from crinoids date back from the Devonian (Fig. 6g; see *Discussion: Processes in the sediments and in the geological record: Echinoderms CaCO_3 accumulation on geological time scales*).

The assessment of the immediate fate of the echinoderm CaCO_3 may be complicated by the controls on carbonate formation and dissolution, which are dependent upon physicochemical and biogeochemical processes (Callender et al. 2002). The echinoderm CaCO_3 particle size (Powell et al. 1986) and burial processes (Powell and Davies 1990, Moran 1992) will exert an impact on carbonate fragmentation and dissolution. Work on molluscs suggested site-specific responses (Reaves 1986) with no CaCO_3 preservation in certain areas, and massive dissolution between 5 and 15 years in others. Rude and Aller (1991) estimated that up to 23% of the CaCO_3 produced by benthic organisms is dissolved by early diagenesis on a time scale of ~ 20 years. These estimates may give a rudimentary idea of the fate of the global echinoderm CaCO_3 , which in any case is not comparable to the mollusks shell carbonate (mainly aragonite; see Davies and Hooper 1962, Comperse and Bates 1973).

Echinoderms CaCO_3 accumulation on geological time scales.—Echinoderms were important carbonate sediment producers from the Palaeozoic to the Mesozoic (Wilkinson 1979, Ausicht 1997). In the modern oceans it is thought that they are not an important biogenic CaCO_3 production compartment (Carozzi and Gerber 1985), although this view is not supported by sediment cores data from the Pliocene (2.5–5.3 million years; C. J. MacLeod, unpublished data; Fig. 6g, h) and the present study. Echinoderm remains preserved in the geological record are ascribed to crinoids (dominant from the Ordovician to the Jurassic, peaking in abundance in the Carboniferous; see Hunter and Zonneveld 2008 and references therein) and to echinoids (e.g., found in sediment cores in the last 5 million years, but present since the Silurian; see Fig. 6g, h). Crinoid remains form a type of rock known as "encrinities," being very common, for example, in North America and the United Kingdom, illustrating Paleozoic accumulations in the fossil record (e.g., Tang et al. 2000). Crinoid accumulations in North America can reach a thickness >10 m, extending over >500 km^2 (Carozzi and Soderman 1962,

Ausicht 1997). Crinoid deposits mainly formed after catastrophic burying events (Meyer and Meyer 1986) in shallow water environments or in deep-sea settings (Hall 1991, Hunter and Zonneveld 2008; see Figs. 5e, f, 6b–d for evidence from present events for other species in shallow and deep waters).

Over the past 600 million years the evolution of biomineralization has been mainly shaped by the adaptation of organisms to external environmental parameters (see Wilkinson 1979 and references therein). Planktonic (mainly coccolithophores and foraminifera) and benthic compartments (green algae and coralline algae, molluscs, corals, brachiopods, bryozoans, and echinoderms) all drove the CaCO_3 accumulation from the Palaeozoic to the present time with different mineralogies arising over time (Johnson 1961, Lipps 1970). Coccolithophores, which are thought to account for the majority of the CaCO_3 exported at present, only contributed significantly from the middle Jurassic, while echinoderms did so from the Silurian. Within the echinoderms there was a switch from CaCO_3 production being dominated by crinoids to echinoids at about the onset of the Jurassic. At present, ophiuroids seem to dominate the carbonate production globally, but they are not commonly recorded in the sediments. Other benthic taxa have contributed greatly to the global marine carbon cycle since the onset of the Mesozoic at about the Triassic (250 millions years ago), and their cumulative carbonate input over time seems much higher than the planktonic organisms (see Wilkinson 1979).

Importance of echinoderm CaCO_3 in large-scale processes

Reassessment of the global CaCO_3 budget.—From our global calculations, the echinoderm standing stocks are ~ 1.84 , 0.24 , and 0.037 Pg CaCO_3 in the shelves, slopes, and abyssal depths, respectively (0.22 , 0.028 , and 0.0044 Pg C as inorganic carbon) ($\text{Pg} = \text{Gt} = 10^{15}$ g). Using these standing stocks and the turnover rates calculated by Smith (1972), echinoderms produce ~ 0.78 , ~ 0.065 , and ~ 0.016 Pg CaCO_3/yr , which translate into ~ 0.093 , ~ 0.0078 , and ~ 0.0019 Pg C/yr as inorganic carbon from the shelves, slopes, and abyssal depths, respectively. These data add to a global total of 0.861 Pg CaCO_3/yr or 0.102 Pg C/yr as inorganic carbon contribution (Table 5). These data are about a factor of two higher than the production rate of 0.047 Pg C/yr calculated for mollusks globally (Chauvaud et al. 2003; Table 5). Our global echinoderm calculations also compare well with the global fish production of CaCO_3 ranging between 0.04 and 0.11 Pg /yr (including magnesium carbonates) recently estimated by Wilson et al. (2009; Table 5). The last estimations from the shelves (where echinoderms may be included) from Milliman and Droxler (1996; updated in Iglesias-Rodriguez et al. 2002), showed production rates similar to these organism-level calculations (Table 5). Values between 0.024 and 0.12 Pg C/yr in the shelves, and 0.06 Pg C/yr as inorganic carbon in the slopes have been obtained from the literature (Table

5). These data are within the range presented here for echinoderms alone as global production rates on an annual basis (0.093 and 0.0078 Pg C/yr from the shelves and slopes, respectively; Table 5). The pelagic CaCO_3 production data included in biogeochemical models of the “biological pump” are also comparable to the echinoderms data (even if arising from different environments; Table 5). The echinoderm global annual production (0.102 Pg C/yr as inorganic carbon) falls below the values for pelagic production (0.6 – 1.6 ± 0.3 Pg C/yr; range \pm SE; e.g., Balch et al. 2007), but it is not negligible at all. The echinoderms production data are above the pelagic foraminifera inorganic carbon flux at 500 m (~ 0.036 – 0.065 Pg C/yr) and that reaching the seabed (0.04 – 0.10 Pg C/yr) (Schiebel 2002). However, the foraminifera fluxes estimated from sediment traps may underestimate the in situ production rate, and in reality the foraminifera production may be higher.

On the sinking side, the echinoderm global carbonate burial rate is complicated to assess. In order to provide an educated guess, the data from Brunskill et al. (2002) suggest that at least in coastal margins, between 60 and 200 g $\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (inorganic carbon) may be deposited annually from carbonate skeletons of echinoderms (among other organisms). Globally the shelves’ inorganic carbon sedimentation rates are between ~ 0.06 and 0.2 Pg C/yr using Brunskill et al. (2002) data. This is comparable to the “accumulation” data (0.17 Pg C/yr) given by Iglesias-Rodriguez et al. (2002) from all the neritic areas. The total inorganic carbon production as CaCO_3 globally from the neritic, slopes, and pelagic areas along with the organism-level data (source) will range between ~ 0.96 and 2.56 Pg C/yr, with net sinks from dissolution and burial in sediments amounting to ~ 1.50 Pg C/yr (Table 5).

Gollety et al. (2008) specifically addressed the need to target neritic areas in terms of inorganic carbon production since they have been particularly ignored in large-scale estimates, even if major secondary production rates have been suggested (e.g., Duarte et al. 2005). This assertion is reinforced by our calculation of the global contributions of echinoderms to the CaCO_3 budget. As a general rule, carbon budgets at large scales are normally derived from models or field data compilations (Feely et al. 2004), while budgets representing ecosystems or organisms need to be addressed and calculated at much smaller scales (e.g., Davoult et al. 1998, Gollety et al. 2008). The data presented here for echinoderms as well as other benthic data sets need to be explicitly addressed and investigated to provide a robust benthic compartment in global biogeochemical models coupled to the biological pump (Lebrato et al. 2009). A prompt incorporation of a benthic compartment, not only including echinoderms, but also other calcifiers such as mollusks, coralline algae, foraminifera, and the like, will certainly improve model outputs and predictions, reducing at the same time the uncertainties in production, export, and sink globally.

TABLE 6. Organism-level and global mean CaCO_3 production rates.

Organism	CaCO_3 production ($\text{g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)†	Location	Reference
Echinoderms	42 ± 84	California	Smith (1972)
Ophiuroid	682	English Channel	Migne et al. (1998)
Polychaet	0.7–397	Mediterranean Sea	Medernach (1996)
Brachiopod	330	Scotland	Collins (1986)
Mollusc	221 ± 184	San Francisco Bay	Chauvaud et al. (2003)
Mollusc	7–64	Florida Bay	Bosence (1989)
Bryozoan	358–1214	Mediterranean Sea	Cocito and Ferdeghini (2001)
Barnacles	481 ± 111 to 1803 ± 467	Brittany	Gollety et al. (2008)
Halimeda	1200	Bahamas	Freile et al. (1995)
Echinoderms‡,§	27.01	global	this study
Halimeda bioherms‡	3000	global	Iglesias-Rodriguez et al. (2002)
Coral reefs‡	1500	global	Iglesias-Rodriguez et al. (2002)
Carbonate shelves‡	20–100	global	Iglesias-Rodriguez et al. (2002)
Slopes‡	1.5	global	Iglesias-Rodriguez et al. (2002)
Pelagic‡	21	global	Li et al. (1969)
Pelagic‡	8	global	Milliman (1993)

† All production rate estimates are as stated in the original paper. Data are sometimes given with a standard deviation, and other times with a range. See reference for the method used in the calculation.

‡ All data were converted from $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ as inorganic carbon to $\text{g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ by multiplying the original values by the CaCO_3/C ratio (8.33).

§ Global mean for all areas and depths. See Table 4 for the shelf, slope, and abyssal depths.

Significance of organism-level measurements in the global CaCO_3 cycle.—Planktonic coccolithophores, foraminifera, and pteropods are traditionally regarded as the taxonomic groups that contribute mostly to the flux of CaCO_3 (calcite and aragonite) from the euphotic zone to the oceans' interior in the biological pump (Lalli and Gilmer 1989, Broerse et al. 2000, Ziveri et al. 2000, Balch et al. 2007). This traditional view of the oceanic CaCO_3 production has been challenged by the suggestion that fish secrete CaCO_3 in their guts, which is then voided to such a large extent as to make an appreciable contribution to the global CaCO_3 flux (~5–15% of global pelagic carbonate production; Wilson et al. 2009). The contribution of other animals such as echinoderms and mollusks has been widely ignored so far as playing a major role in the global CaCO_3 cycle. This study estimates a global CaCO_3 production from echinoderms in all areas to be $>25 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and $>70 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for the shelves (Table 6). These estimates are below the regional flux estimation from ophiuroids of Megne et al. (1998) in the English Channel (Table 6), with a mean of $682 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. However, some regional production calculations in our study were $>1000 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ from ophiuroids, which are well above what is normally recorded in the literature for macrobenthic communities. This reinforces the role of echinoderms in the production side in the global CaCO_3 budget. Their production rates are above regional production calculations from Smith (1972) benthic community estimate of $400 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ off California, USA ($42 \pm 84 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ for echinoderms production), Medernach (1996) polychaete community production in the Mediterranean Sea, and the brachiopod assemblages studied by Collins (1986) in Scotland (Table 6). The echinoderms data are similar at a

regional level to Chauvaud et al. (2003) calculations from clams, with a maximum production of $1100 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (mean of $221 \pm 184 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) in San Francisco Bay, California, USA (Table 6). Other organism-level calculations include bryozoans in the Mediterranean Sea, which cover substantial parts of the benthos with CaCO_3 production rates between 358 and $1214 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Cocito and Ferdeghini 2001; Table 6). Rocky-shore invertebrates such as barnacles may produce between 400 and $1800 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Gollety et al. 2008). The reduced global areal cover of barnacles beyond hard substrata in the neritic areas may render them a minor contributor to the global CaCO_3 cycle. However, their production should not be ignored in regional calculations due to the high production rate per unit area. Lastly, coral reef and Halimeda bioherms bear some of the highest global production rates, where their contributions have already been well assessed (Table 6).

Our global echinoderm production rate from the shelf ($77.91 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) is within the range provided by Iglesias-Rodriguez et al. (2002) for the carbonate shelves (~20–100 $\text{g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). However, our calculation for the slopes ($2.05 \text{ g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) is below the one provided in the literature (~15 $\text{g CaCO}_3 \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). The slope is a very poorly sampled area in terms of carbon cycling processes, which need further detailed study. These results illustrate an emerging need for an adequate characterization of the CaCO_3 inventories in all the benthic areas (neritic, shelf, slope, and abyssal) including calcifying organisms on a global scale. To achieve this, organism-level measurements in combination with physicochemical analysis of the surrounding water are fundamental to provide a global representation of the echinoderm contribution to

the CaCO_3 budget on shelves, slopes, and other deep-sea areas.

Potential effects of shallowing Ω -Ca horizons on echinoderms CaCO_3 inventories

Shallow water echinoderms in the Atlantic Ocean are not expected to encounter undersaturated waters in the next few decades (see Fig. 4), but for deep-sea and polar populations the situation may be different (Orr et al. 2005). Howell et al. (2002) recorded 47 asteroid species in the northeast Atlantic between 150 and 4950 m depth, with nine of them occurring at maximum abundance between 4000 and 5000 m. Ω -Ca undersaturation occurs in the Atlantic Ocean deeper than \sim 4500 m (Fig. 4; see also Feely et al. 2004), which means that a few deep-sea asteroids already inhabit undersaturated waters. The question is whether or not shallower water species with very restricted bathymetric ranges (e.g., 200–300 m; Howell et al. 2002) will be able to withstand calcium carbonate undersaturation. It appears that $>80\%$ of the global CaCO_3 standing stocks from echinoderms occur between 0 and 800 m. However, the saturation horizons are shallower in the South Atlantic (see Fig. 4), and thus the fate of echinoderm populations there remains an open question. In the Mediterranean Sea and in other enclosed basins, the water masses remain saturated with respect to calcite down to the seabed, and they are more highly saturated than Atlantic water at the same depth (Miller et al. 1979). This is due to lower pH in the deep Atlantic waters as a consequence of much higher organic supply and subsequent remineralization.

The situation in the Southern Ocean (Antarctic region) is difficult to predict, since animals there may be very sensitive to changing conditions (Arntz et al. 1994, Orr et al. 2005). Antarctic animals are very sensitive to small biological changes that can affect their long-term survival capacities (Peck et al. 2004). Watson et al. (2008) reported that the shell of an Antarctic echinoid (*Sterechinus neumayeri*) was 15% thinner than a temperate species (*Psammechinus miliaris*). A thinner shell in Antarctic species may be a consequence of the elemental concentrations (mainly magnesium and calcium) in the surrounding waters as seen for coccolithophores and corals (see Stanley et al. 2005, Ries et al. 2006). A priori, these animals may be even more susceptible, but the data from Clark et al. (2009) on sea urchin Antarctic larvae (*S. neumayeri*) at high CO_2 reveal the contrary. At pH levels reduced to 6.5, the Antarctic larvae were the least affected (in terms of survival and calcification) in comparison with other equatorial and mid-latitude species. This may be a consequence of evolution in a natural high- CO_2 environment, enabling the animals to be adapted to those conditions, making them actually more resilient. In the Arctic, at present there are not enough data to draw a conclusion, but surface areas in the subarctic Pacific, north of 60° N are close to undersaturation.

In the Pacific Ocean, saturation horizons are shallow north of 40° N, and in some places near the equator (Fig. 4; see Feely et al. 2004, 2008, Fabry et al. 2008). In areas such as the Gulf of Alaska, where dense populations of echinoderms are recorded (Fig. 4), undersaturation may be achieved at <300 m. Feely et al. (2008) also reported on the upwelling of undersaturated waters off California, from 26 – 52° N. At present, these undersaturation events are highly seasonal (Feely et al. 2008) but are predicted to become common as a result of the anthropogenic emissions of CO_2 . It is desirable to ascertain if future increases in the duration, range, and intensity of undersaturated waters will affect both echinoderm survivorship and what effect this will have on the global CaCO_3 budget. If a reduction in calcification or survival is widely found in echinoderms, as it has been observed in the majority of experiments carried out to date with organisms other than echinoderms (Langdon et al. 2003, Kleypas et al. 2006, Gazeau et al. 2007), their contribution to the CaCO_3 inventory may be diminished, especially in the north Pacific. The data from Clark et al. (2009) indicate a reduction in calcification between 10% and 40% in sea urchin larvae of three species from the southern hemisphere, except in an Antarctic one. Unless we have more information across all latitudes it will be impossible to predict the echinoderms CaCO_3 production and export in the future. However, the main way of reducing their contribution to the CaCO_3 budget is through physiological failure (survival and development) and the impossibility to recruit to adult populations due to mortality at larval stages. Dupont et al. (2008) found 100% mortality in ophiuroid larvae at a pH of between 7.9 and 7.7, as well as abnormal skeletogenesis. These pH values were well above Ω -Ca undersaturation (e.g., Ω -Ca = 2.57 at pH = 7.9, and Ω -Ca = 1.7 at pH = 7.7; S. Dupont, *personal communication*). However, whether Ω -Ca = 1 represents a tipping point for skeletogenesis remains an open question. Dupont and Thorndyke (2009) present larval survival responses from 17 echinoderm species, with seven of them showing reduced survival in response to increased CO_2 and reduced Ω -Ca, and three showing increased survival. They also show a negative effect on larval body development in 16 of the 17 species in response to increased CO_2 and reduced Ω -Ca. The response of echinoderms larvae may be species specific (e.g., Clark et al. 2009), and the main effect seems to be in terms of survival and developmental dynamics (Dupont and Thorndyke 2009). A decrease in recruitment as low as 1% per generation may reduce adult populations substantially in the long-term (Dupont et al. 2008), ultimately affecting their CaCO_3 contribution.

The potential for inorganic carbon dissolution in echinoderms may be exacerbated since many species incorporate high magnesium calcite (>5 mole% MgCO_3 ; e.g., Weber 1969, Dickson 2002), which is more soluble than aragonite (Bischoff et al. 1987). The saturation

state of water with respect to high magnesium calcite is much lower than that of calcite or aragonite (Morse et al. 2006, Andersson et al. 2008). This could affect even more the contribution of high-magnesium calcite taxa such as echinoderms. However, data from Wood et al. (2008) indicate that adult ophiuroids may increase calcification rates in a high CO₂ world. Seemingly, data from Gooding et al. (2009) combining CO₂ and temperature show an increase in growth rate of a starfish. Even more complicated is the response of a sea urchin larvae presented by Byrne et al. (2009), where CO₂ did not have any effect on gastrulation or development, but temperature alone affected both processes. These complex responses, especially in multifactorial experiments combining high CO₂ with high temperature, prevent us from predicting predominantly linear responses to ocean acidification, which seem to be species specific (Clark et al. 2009). This taxonomical response has also been discussed by Fabry et al. (2008) based on the Ries et al. (2008) study, which presented both positive and negative as well as parabolic relationships in calcification for benthic invertebrates under high CO₂. Beyond experimental data, it is proposed that changes in the upper ocean biogeochemistry influenced by both CO₂ and temperature, may alter the ultimate food supply to benthic ecosystems by reducing the POC flux as a consequence of declines in primary production (e.g., Buesseler et al. 2007), especially in deep-sea areas (Smith et al. 2008). Echinoderms, which dominate many of these areas, may be affected (declining in density) by reducing the quality of their food or their reproductive success. These results, particularly those showing nonlinear patterns or indirect effects, need to be carefully examined if we are to understand mechanisms that drive the future global CaCO₃ cycle. Unless we have a clear pattern of response in a high CO₂ world (very unlikely), it will be difficult to derive equations to predict future changes in the carbon exported by echinoderms and other benthic compartments, if we wish to incorporate this knowledge into the global biogeochemical models coupled to the biological pump. Additionally, as more experimental work is done and more data are gathered on both pelagic and benthic organisms responses, it is becoming obvious that we need to make a profound reassessment and to reconsider of our “presumed knowledge” both on the ocean acidification field and on the global biogeochemical cycles and processes associated to the biological pump.

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LITERATURE CITED

- Andersson, A. J., F. T. Mackenzie, and N. R. Bates. 2008. Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Marine Ecology Progress Series* 373:265–273.
- Anger, K., U. Rogal, G. Schriever, and C. Valentin. 1977. In situ investigations on the echinoderm *Asterias rubens* as a predator of soft bottom communities in the western Baltic Sea. *Helgoländer wiss Meeresunters* 29:439–459.
- Anikouche, W. A., and R. W. Sternberg. 1973. The world ocean. An introduction to oceanography. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Arntz, W. E., T. Brey, and V. A. Gallardo. 1994. Antarctic zoobenthos. *Oceanography and Marine Biology Annual Review* 32:241–304.
- Ausicht, W. I. 1997. Regional encrinites: a vanished lithofacies. Pages 509–519 in C. E. Brett and G. C. Baird, editors. *Paleontological events: stratigraphic, ecologic and evolutionary implications*. Columbia University Press, New York, New York, USA.
- Balch, W. M., D. T. Drapeau, B. C. Bowler, and E. Booth. 2007. Prediction of pelagic calcification rates using satellite measurements. *Deep-Sea Research II* 54:478–495.
- Barnes, A. T., L. B. Quetin, J. J. Childress, and D. L. Pawson. 1976. Deep-sea macroplanktonic sea cucumbers; suspended sediment feeders captured from deep submergence vehicle. *Science* 194:1083–1085.
- Bauer, J. C., and C. M. Young. 2000. Epidermal lesions and mortality caused by vibriosis in deep-sea Bahamian echinoids: a laboratory study. *Diseases of Aquatic Organisms* 39: 193–199.
- Berelson, W. M., R. F. Anderson, J. Dymond, D. DeMaster, D. E. Hammond, R. Collier, S. Honjo, M. Leinen, J. McManus, R. Pope, C. Smith, and M. Stephens. 1997. Biogenic budgets of particle rain, benthic remineralization and sediment accumulation in the equatorial Pacific. *Deep-Sea Research II* 44:2251–2282.
- Berelson, W. M., W. M. Balch, R. A. Feely, C. Sabine, and K. Lee. 2007. Relating estimates of CaCO₃ production, export, and dissolution in the water column to measurements of CaCO₃ rain into sediment traps and dissolution on the sea floor: a revised global carbonate budget. *Global Biogeochemical Cycles* 21:GB1024.
- Bergman, M. J. N., M. Fonds, A. Hup, and A. Stam. 1990. Direct effects of beam trawl fishing on benthic fauna in the North Sea. *ICES Journal of Marine Science* 11.
- Bertram, M. A., F. T. Mackenzie, F. C. Bishop, and W. D. Bischoff. 1991. Influence of temperature on the stability of magnesian calcite. *American Mineralogist* 76:1889–1896.
- Billett, D. S. M. 1991. Deep-sea holothurians. *Oceanography and Marine Biology: an Annual Review* 29:259–317.
- Billett, D. S. M., B. J. Bett, A. L. Rice, M. H. Thurston, J. Galeron, M. Sibuet, and G. A. Wolff. 2001. Long-term

- changes in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Progress in Oceanography* 50:325–348.
- Billett, D. S. M., and B. Hansen. 1982. Abyssal aggregations of *Kolga hyalina* Danielssen and Koren (Echinodermata: Holothuroidea) in the northeast Atlantic Ocean: a preliminary report. *Deep-Sea Research I* 29:799–818.
- Bischoff, W. D., F. T. Mackenzie, and F. C. Bishop. 1987. Stabilities of synthetic magnesian calcites in aqueous solution: comparison with biogenic materials. *Geochimica et Cosmochimica Acta* 51:1413–1423.
- Blaber, S. J. M., N. J. May, J. W. Young, and C. M. Bulman. 1987. Population density and predators of *Ophiacantha fidelis* (Koehler, 1930) (Echinodermata: Ophiuroidea) on the continental slope of Tasmania. *Australian Journal of Marine Freshwater Research* 38:243–247.
- Bluhm, B. A., D. Piepenburg, and K. von Juterzenka. 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. *Polar Biology* 20:325–334.
- Bosence, D. W. J. 1989. Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science* 44:419–433.
- Brey, T., and J. Gutt. 1991. The genus *Sterechinus* (Echinodermata: Echinoidea) on the Weddell sea shelf and slope (Antarctica): distribution, abundance and biomass. *Polar Biology* 11:227–232.
- Broerse, A. T. C., G. J. A. Brummer, and J. E. van Hinte. 2000. Coccolithophore export production in response to monsoonal upwelling off Somalia (northwestern Indian Ocean). *Deep-Sea Research II* 47:2179–2205.
- Brunskill, G. J., I. Zagorskis, and J. Pfitzner. 2002. Carbon burial rates in sediments and a carbon mass balance for the Herbert river region of the Great Barrier Reef continental shelf, north Queensland, Australia. *Estuarine, Coastal and Shelf Science* 54:677–700.
- Buesseler, K. O., et al. 2007. Revisiting carbon flux through the ocean's twilight zone. *Science* 316:567–570.
- Bullock, T. H. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biological Reviews* 30:311–342.
- Byrne, M., and A. Davis. 2008. The acid test: responses of benthic invertebrates to climate change. *Australian Antarctic Magazine* 15:8–9.
- Byrne, M., M. Ho, P. Selvakumaraswamy, H. D. Nguyen, S. A. Dworjanyn, and A. R. Davis. 2009. Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *Proceedings of the Royal Society B* 276:1883–1888.
- Caldeira, K., and M. E. Wickett. 2005. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *Journal of Geophysical Research* 110:C09S04.
- Callender, W. R., G. M. Staff, K. M. Parsons-Hubbard, E. N. Powell, G. T. Rowe, S. E. Walker, C. E. Brett, A. Raymond, D. D. Carlson, S. White, and E. A. Heise. 2002. Taphonomic trends along a fore-reef slope: Lee Stocking Island, Bahamas: I. Location and water depth. *PALAIOS* 17:50–65.
- Carozzi, A. V., and M. S. Gerber. 1985. Crinoid arenite banks and crinoid wacke inertia flows: a depositional model for the Burlington Limestone (middle Mississippian), Illinois, Iowa, and Missouri, USA. Pages 452–460 in E. S. Belt and R. W. MacQueen, editors. *Congress International de Stratigraphie et de Geologie du Carbonifere. Compte Rendu 3*. Southern Illinois University Press, Carbondale, Illinois, USA.
- Carozzi, A. V., and J. G. W. Soderman. 1962. Petrography of Mississippian (Borden) crinoidal limestones at Stobo, Indiana. *Journal of Sedimentary Research* 32:397–414.
- Cartes, J. E. 1994. Influence of depth and seasonality on the diet of the deep-water aristeid *Aristeus antennatus* along the continental slope (400 to 2300 m) in the Catalan Sea (western Mediterranean). *Marine Biology* 120:639–648.
- Cartes, J. E., F. Maynou, E. Fanelli, C. Romano, V. Mamouridis, and V. Papi. 2009. The distribution of megabenthic, invertebrate epifauna in the Balearic Basin (western Mediterranean) between 400 and 2300 m: environmental gradients influencing assemblages composition and biomass trends. *Journal of Sea Research* 61:244–257.
- Catubig, N. R., D. E. Archer, R. Francois, P. de Penocal, W. Howard, and E. F. Yu. 1998. Global deep-sea burial rate of calcium carbonate during the last glacial maximum. *Paleoceanography* 13:298–310.
- Chauvaud, L., J. K. Thompson, J. E. Cloern, and G. Thouzeau. 2003. Clams as CO₂ generators: the *Potamocorbula amurensis* example in San Francisco Bay. *Limnology and Oceanography* 48:2086–2092.
- Chiappone, M., D. W. Swanson, and S. L. Miller. 2002. Density, spatial distribution and size structure of sea urchins in Florida Keys coral reef and hard-bottom habitats. *Marine Ecology Progress Series* 235:117–126.
- Clark, A. M., and M. E. Downey. 1992. Starfishes of the Atlantic. Natural History Museum Publications, Chapman and Hall, London, UK.
- Clark, D., M. Lamare, and M. Barker. 2009. Response of sea urchin larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate and a polar species. *Marine Biology* 156:1125–1137.
- Cocito, S., and F. Ferdeghini. 2001. Carbonate standing stock and carbonate production of the bryozoan *Pentapora fascialis* in the north-western Mediterranean. *Facies* 45:25–30.
- Collins, M. J. 1986. Taphonomic processes in a deep water *Modiolus*-brachiopod assemblage from the west coast of Scotland. Dissertation. University of Glasgow, Glasgow, Scotland.
- Comperse, E. L., and J. M. Bates. 1973. Determination of calcite : aragonite ratios in mollusc shells by infrared spectra. *Limnology and Oceanography* 18:326–331.
- Cosson, N., M. Sibuet, and J. Galeron. 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. *Deep-Sea Research I* 44:247–269.
- David, B., T. Chone, A. Festeau, R. Mooi, and C. de Ridder. 2005. Biodiversity of Antarctic echinoids: a comprehensive and interactive database. *Scientia Marina* 69:201–203.
- Davies, T. T., and P. R. Hooper. 1962. The determination of the calcite:aragonite ratio in mollusc shells by X-ray diffraction. *Mineralogy Magazine* 33:608–612.
- Davoult, D., N. Degros, M. A. Janquin, and B. Soyez. 1992. Biometrics, carbon and nitrogen content in the ophiuroids *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom* 72:915–918.
- Davoult, D., F. Dewailly, and A. Migne. 1998. Carbon and nitrogen budget of a dense population of the suspension feeding ophiuroids *Ophiothrix fragilis* in a coastal ecosystem. Pages 337–342 in R. Mooi and M. Telford, editors. *Echinoderms: San Francisco*. Balkema, Rotterdam, The Netherlands.
- Dickson, A. G. 1990. Standard potential of the reaction: $\text{AgCl(s)} + 1/2 \text{H}_2(\text{g}) = \text{Ag(s)} + \text{HCl(aq)}$, and the standard acidity constant of the ion HSO_4^- in synthetic sea water from 273.15 to 318.15 K. *Journal of Chemical Thermodynamics* 22:113–127.
- Dickson, A. G., and F. J. Millero. 1987. A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. *Deep-Sea Research I* 36:1733–1743.
- Dickson, J. A. D. 2002. Fossil echinoderms as monitor of the Mg/Ca ratio of Phanerozoic oceans. *Science* 298:1222–1224.
- Doney, S. C., V. J. Fabry, R. A. Feely, and J. A. Kleypas. 2009. Ocean acidification: the other CO₂ problem. *Annual Review of Marine Science* 1:169–192.
- Duarte, C. M., J. J. Middelburg, and N. F. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2:1–8.

- Dupont, S., J. Havenhand, J. W. Thorndyke, L. Peck, and M. C. Thorndyke. 2008. Near-future level of CO₂-driven radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Marine Ecology Progress Series* 373:285–294.
- Dupont, S., and M. C. Thorndyke. 2009. Impact of CO₂-driven ocean acidification on invertebrates early life-history. What we know, what we need to know and what we can do. *Biogeosciences Discussions* 6:3109–3131.
- Ebert, T. A., and M. P. Russell. 1992. Growth and mortality estimates for red sea urchin *Strongylocentrotus franciscanus* from San Nicolas Island, California. *Marine Ecology Progress Series* 81:31–41.
- Ellis, J. R., and S. I. Rogers. 2000. The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel and Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 80:127–138.
- Fabry, V. J., B. A. Seibel, R. A. Feely, and J. C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65: 414–432.
- Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320: 1490–1492.
- Feely, R. A., C. L. Sabine, K. Lee, W. Berelson, J. Kleypas, V. J. Fabry, and F. J. Millero. 2004. Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305:362–366.
- Franz, D. R., E. K. Worley, and A. S. Merrill. 1981. Distribution patterns of common seastars of the Middle Atlantic Continental shelf of the Northwest Atlantic (Gulf of Maine to Cape Hatteras). *Biological Bulletin* 160:394–418.
- Freile, D., J. D. Milliman, and L. Hillis. 1995. Leeward bank margin *Halimeda* meadows and draperies and their sedimentary importance on the western Great Bahama Bank slope. *Coral Reefs* 14:27–33.
- Fujita, T., and S. Ohta. 1989. Spatial structure within a dense bed of the brittle star *Ophiura sarsii* (Ophiuroidea: Echinodermata) in the bathyal zone off Otsuchi, northeastern Japan. *Journal of the Oceanographical Society of Japan* 45: 289–300.
- Fujita, T., and S. Ohta. 1990. Size structure of dense populations of the brittle star *Ophiura sarsi* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. *Marine Ecology Progress Series* 64:113–122.
- Gage, J. D., and P. A. Tyler. 1991. *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge University Press, Cambridge, UK.
- Gangstø, R., M. Gehlen, B. Schneider, L. Bopp, O. Aumont, and F. Joos. 2008. Modeling the marine aragonite cycle: changes under rising carbon dioxide and its role in shallow water CaCO₃ dissolution. *Biogeosciences* 5:1057–1072.
- Garcia, J., H. M. Yeh, and S. Ohta. 2002. Distribution and bathymetric zonation of deep-sea brittle stars (Echinodermata: Ophiuroidea) off the Japanese Pacific coast. *Journal of the Marine Biological Association of the United Kingdom* 82:345–346.
- Gattuso, J. P., M. Frankignoulle, I. Bourge, S. Romaine, and R. W. Buddemeier. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* 18:37–46.
- Gazeau, F., C. Quiblier, J. M. Jansen, J. P. Gattuso, J. J. Middelburg, and C. H. R. Heip. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letters* 34:L07603.
- Gehlen, M., R. Gangstø, B. Schneider, L. Bopp, O. Aumont, and C. Ethe. 2007. The fate of pelagic CaCO₃ production in a high CO₂ ocean: a model study. *Biogeosciences* 4:505–519.
- Glynn, P. W. 1984. Widespread coral mortality and the 1982–83 El Niño warming event. *Environmental Conservation* 11: 133–146.
- Gollety, C., F. Gentil, and D. Davoult. 2008. Secondary production, calcification and CO₂ fluxes in the cirripedes *Chthamalus montagui* and *Elminius modestus*. *Oecologia* 155: 133–142.
- Gooding, R. A., C. D. G. Harley, and E. Tang. 2009. Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *Proceedings of the National Academy of Sciences USA* 106:9316–9321.
- Griffith, S. P., R. P. Garcia, and E. Weil. 2003. Bioerosion in coral reef communities in southwest Puerto Rico by the sea urchin *Echinometra viridis*. *Marine Biology* 143:79–84.
- Gutt, J. 1988. On the distribution and ecology of sea cucumbers (Holothuroidea, Echinodermata) in the Weddell Sea (Antarctica). *Berichte zur Polarforschung* 41:1–87.
- Gutt, J. 1991. Are Weddell Sea holothurians typical representatives of the Antarctic benthos? *Meeresforschung* 33:312–329.
- Gutt, J., and M. Klages. 1991. In situ observations on the genus *Bathyploetes* (Holothuroidea, Echinodermata) in Antarctica and its relevance to taxonomy. *Zoologica Scripta* 20:301–306.
- Haderlie, E. C. 1969. Marine fouling and boring organisms in Monterey Harbor II. Second year of investigation. *Veliger* 12:182–192.
- Haedrich, R. L., and J. E. Maunder. 1984. The echinoderm fauna of the Newfoundland continental slope. Pages 37–46 in B. F. Keegan and B. D. S. O'Connor, editors. *Proceedings of the Fifth International Echinoderm Conference*, Galway, Ireland. A. A. Balkema, Rotterdam, The Netherlands.
- Haedrich, R. L., G. T. Rowe, and P. T. Polloni. 1980. The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology* 57:165–179.
- Hall, R. L. 1991. *Seirocrinus subangularis* (Miller, 1821), a Pliensbachian (Lower Jurassic) crinoid from the Fernie Formation, Alberta, Canada. *Journal of Paleontology* 65: 300–307.
- Harris, R. J. C. 1954. *Biological applications of freezing and drying*. Academic Press, New York, New York.
- Hendler, G., and D. L. Meyer. 1982. Ophiuroids flagrante delicto and notes on the spawning behavior of other echinoderms in their natural habitat. *Bulletin of Marine Science* 32:600–607.
- Honjo, S., S. J. Manganini, R. A. Krishfield, and R. Francois. 2008. Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: a synthesis of global sediment trap programs since 1983. *Progress in Oceanography* 76:217–285.
- Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu. 2001. *Climate Change 2001: the scientific basis: contributions of Working Group I to the third assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Howell, K. L., D. S. M. Billett, and P. A. Tyler. 2002. Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N. E. Atlantic. *Deep-Sea Research I* 49:1901–1920.
- Hudson, I. R., B. D. Wigham, and P. A. Tyler. 2004. The feeding behavior of a deep-sea holothurian, *Stichopus tremulus* (Gunnerus) based on *in situ* observations and experiments using a remotely operated vehicle. *Journal of Experimental Marine Biology and Ecology* 301:75–91.
- Hunte, W., I. Cote, and T. Tomascik. 1986. On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. *Coral Reefs* 4:135–139.
- Hunter, A. E., and J.-P. Zonneveld. 2008. Palaeoecology of Jurassic encrinites: reconstructing crinoid communities from

- the Western Interior Seaway of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263:58–70.
- Iglesias-Rodriguez, M. D., R. Armstrong, R. A. Feely, R. Hood, J. Kleypas, J. D. Milliman, C. Sabine, and J. Sarmiento. 2002. Progress made in the study of ocean's calcium carbonate budget. *EOS Transactions, American Geophysical Union* 83:374–375.
- IOC, IHO, and BODC. 2003. Centenary Edition of the GEBCO Digital Atlas, published on CD-ROM on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans. British Oceanographic Data Centre, Liverpool, UK.
- Isaji, S. 1995. Defensive strategies against shell dissolution in bivalves inhabiting acidic environments: the case of *Geloina* (Corbiculidae) in mangrove swamps. *Veliger* 38:235–246.
- Jahnke, R. A. 1996. The global ocean flux of particulate organic carbon: areal distribution and magnitude. *Global Biogeochemical Cycles* 10:71–88.
- Johnson, J. H. 1961. Limestone-building algae and algal limestones. Colorado School of Mines, Golden, Colorado, USA.
- Johnson, K. M. 1995. Operator's manual. Single-operator multiparameter metabolic analyzer (SOMMA) for total carbon dioxide (C_T) with Coulometric detection. Version 3.0. Department of Applied Science, Brookhaven National Laboratory, Upton, New York, New York, USA.
- Johnson, K. M., A. G. Dickson, G. Eischeid, C. Goyet, P. Guenther, R. M. Key, F. J. Millero, D. Purkerson, C. L. Sabine, R. G. Schottle, D. W. L. Wallace, R. J. Wilke, and C. D. Winn. 1998. Coulometric total carbon dioxide analysis for marine studies: assessment of the quality of total inorganic carbon measurements made during the US Indian Ocean CO Survey 1994–1996. *Marine Chemistry* 63:21–37.
- Jones, D. O. B., B. J. Bett, and P. A. Tyler. 2007. Depth related changes to density, diversity and structure of benthic megafaunal assemblages in the Fimbul ice shelf region, Weddell Sea, Antarctica. *Polar Biology* 30:1579–1592.
- Jutterström, S., and L. G. Anderson. 2005. The saturation of calcite and aragonite in the Arctic Ocean. *Marine Chemistry* 94:101–110.
- Kenner, M. C., and M. T. Lares. 1991. Size at first reproduction of the sea urchin *Strongylocentrotus purpuratus* in a central California kelp forest. *Marine Ecology Progress Series* 76: 303–306.
- Key, R. M., A. Kozyr, C. L. Sabine, K. Lee, R. Wanninkhof, J. L. Bullister, R. A. Feely, F. J. Millero, C. Mordy, and T. H. Peng. 2004. A global ocean carbon climatology: results from global data analysis project (GLODAP). *Global Biogeochemical Cycles* 18:GB4031.
- Kleypas, J. A., R. A. Feely, V. J. Fabry, C. Langdon, C. L. Sabine, and L. L. Robbins. 2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a workshop held 18–20 April 2005, St. Petersburg, Florida, sponsored by NSF, NOAA, and the U.S. Geological Survey. (<http://www.isse.ucar.edu/florida/>)
- Kurihara, H., and Y. Shirayama. 2004. Effects of increased atmospheric CO_2 on sea urchin early development. *Marine Ecology Progress Series* 274:161–169.
- Lalli, C. M., and R. W. Gilmer. 1989. Pelagic snails: the biology of holoplanktonic gastropod mollusks. Stanford University Press, Stanford, California, USA.
- Lampitt, R. S., and A. N. Antia. 1997. Particle flux in deep seas: regional characteristics and temporal variability. *Deep-Sea Research I* 44:1377–1403.
- Lampitt, R. S., B. J. Bett, K. Kiriakoulakis, E. E. Popova, O. Ragueneau, A. Vangriesheim, and G. A. Wolff. 2001. Material supply to the sea floor in the Northeast Atlantic. *Progress in Oceanography* 50:27–63.
- Langdon, C., W. S. Broecker, D. E. Hammond, E. Glenn, K. Fitzsimmons, S. G. Nelson, T. H. Peng, I. Hajdas, and G. Bonani. 2003. Effect of elevated CO_2 on the community metabolism of an experimental coral reef. *Global Biogeochemical Cycles* 17:1011.
- Lawrence, J. M. 2007. Edible sea urchins: biology and ecology. Elsevier, Amsterdam, The Netherlands.
- Lebrato, M., A. Oschlies, D. Iglesias-Rodriguez, J.-P. Gattuso, A.-M. Nisumaa, M. N. Müller, K. G. Schulz, S. Hohn, and C. Hauri. 2009. From organism responses to biogeochemical impacts: global meta-analysis of experimental data. Proceedings of the EPOCA First Annual Meeting, Plymouth, UK.
- Lee, K. 2001. Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. *Limnology and Oceanography* 46:1287–1297.
- Lessios, H. A., J. D. Cubit, D. R. Robertson, M. J. Shulman, M. R. Parker, S. D. Garrity, and S. C. Levings. 1984a. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* 3:173–182.
- Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984b. Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335–337.
- Lewis, E., and D. W. R. Wallace. 1998. Program developed for CO_2 system calculations. ORNL/CDIAC-105. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.
- Lewis, J. B., and G. S. Storey. 1984. Differences in morphology and life history traits of the echinoid *Echinometra lucunter* from different habitats. *Marine Ecology Progress Series* 15: 207–211.
- Li, Y. H., T. Takahashi, and W. S. Broecker. 1969. Degree of saturation of $CaCO_3$ in the oceans. *Journal of Geophysical Research* 74:5507–5525.
- Lipps, J. H. 1970. Plankton evolution. *Evolution* 24:1–21.
- MacLeod, C. J., et al. 1998. Geological mapping of slow-spread lower ocean crust: a deep-towed video and wireline rock drilling survey of Atlantis Bank (ODP Site 735, SW Indian Ridge). *InterRidge News* 7:39–43.
- MacLeod, C. J., et al. 2000. Tectonic evolution and uplift/subsidence history of Atlantis Bank, a transverse ridge near the Atlantis II Fracture Zone, SW Indian Ridge. *EOS Transactions AGU* 81:F1129.
- Marshall, N. B. 1979. Developments in deep-sea biology. Blandford Press, Poole, England.
- Marubini, F., C. Ferrier-Pages, P. Furla, and D. Allemand. 2008. Coral calcification responds to seawater acidification: a working hypothesis toward a physiological mechanism. *Coral Reefs* 27:491–499.
- Maxwell, W. G. H. 1971. Echinoderm debris from Great Barrier Reef sediment, distribution and age. Pages 43–45 in R. J. Walsh, C. L. Harris, J. M. Harvey, W. G. H. Maxwell, J. M. Thomson, and D. J. Tranter, Report of the committee on the problem of the crown-of-thorns starfish (*Acanthaster planci*). CSIRO, Melbourne, Australia.
- Mayer, M., and D. Piepenburg. 1996. Epibenthic community patterns on the continental slope off East Greenland at 75°N. *Marine Ecology Progress Series* 143:151–164.
- McCarthy, D., and C. M. Young. 2002. Seasonal reproduction and gametogenesis in the echinoid *Lytechinus variegatus*. *Marine Ecology Progress Series* 233:157–168.
- Messing, C. G. 1994. Comatulid crinoids (Echinodermata) of Madang, Papua New Guinea, and environs: diversity and ecology. Pages 237–243 in B. David, A. Guille, J.-P. Feral, and M. Roux, editors. Echinoderms through time. Balkema, Rotterdam, The Netherlands.
- McClintock, J. B. 1994. Trophic biology of Antarctic shallow water echinoderms. *Marine Ecology Progress Series* 111:191–202.

- McClintock, J. B., and J. S. Pearse. 1987. Biochemical composition of Antarctic echinoderms. *Comparative Biochemistry and Physiology* 86:683–687.
- Medernach, L. 1996. Biogeography and secondary production of the polychaete *Ditrupa antenia* along the French-Catalan coast. DEA, University of Paris VI, Paris, France. [In French.]
- Mehrbach, C., C. H. Cuberson, J. E. Hawley, and R. M. Pytkowicz. 1973. Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnology and Oceanography* 18:897–907.
- Menge, B. A. 1979. Coexistence between the seastar *Asterias vulgaris* and *Asterias forbesi* in a heterogeneous environment: a non-equilibrium explanation. *Oecologia* 41:245–272.
- Metaxas, A., and B. Giffin. 2004. Dense beds of the ophiuroid *Ophiacantha abyssicola* on the continental slope off Nova Scotia, Canada. *Deep-Sea Research I* 51:1307–1317.
- Meyer, D. L., and K. B. Meyer. 1986. Biostratinomy of recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia. *PALAIOS* 1:294–301.
- Migne, A., D. Davout, and J. P. Gattuso. 1998. Calcium carbonate production of a dense population of the brittlestar *Ophiolithrix fragilis* (Echinodermata: Ophiuroidea): role of the carbon cycle of a temperate coastal ecosystem. *Marine Ecology Progress Series* 173:305–308.
- Millero, F. J., J. W. Morse, and C. T. Chen. 1979. The carbonate system in the western Mediterranean Sea. *Deep-Sea Research I* 26:1395–1404.
- Milliman, J. D. 1993. Production and accumulation of calcium carbonate in the ocean: budget of a non-steady state. *Global Biogeochemical Cycles* 7:927–957.
- Milliman, J. D., and A. W. Droxler. 1995. Calcium carbonate sedimentation in the global ocean: linkages between the neritic and pelagic environments. *Oceanography* 8:92–95.
- Milliman, J. D., and A. W. Droxler. 1996. Neritic and pelagic carbonate sedimentation in the marine environment: ignorance is not bliss. *Geologische Rundschau* 85:496–504.
- Moore, J. K., S. C. Doney, and K. Lindsay. 2004. Upper ocean ecosystem dynamics and iron cycling in a global three dimensional model. *Global Biogeochemical Cycles* 18:GB4028.
- Moran, P. J. 1992. Preliminary observations of the decomposition of crown-of-thorns starfish, *Acanthaster planci*. *Coral Reefs* 11:115–118.
- Morse, J. W., A. J. Andersson, and F. T. Mackenzie. 2006. Initial responses of carbonate-rich shelf sediments to rising atmospheric pCO₂ and “ocean acidification”: role of high Mg-calcites. *Geochimica et Cosmochimica Acta* 70:5814–5830.
- Orr, J. C., et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686.
- Pawson, D. L. 2007. Phylum Echinodermata. *Zootaxa* 1668:749–764.
- Pearce, C. M., S. Williams, F. Yuan, J. D. Castell, and S. M. C. Robinson. 2005. Effect of temperature on somatic growth and survivorship of early post-settled green sea urchin *Strongylocentrotus droebachiensis*. *Aquaculture Research* 36:600–609.
- Peck, L. S., K. E. Webb, and D. M. Bailey. 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology* 18:625–630.
- Péres, J. M. 1985. History of the Mediterranean biota and the colonization of the depths. Pages 198–232 in R. Margalef, editor. *Key environments: Western Mediterranean*. Pergamon Press, New York, New York, USA.
- Picken, G. B. 1985. Benthic research in Antarctica: past, present and future. Pages 167–184 in J. S. Gray and M. E. Christiansen, editors. *Marine biology of polar regions and effects of stress on marine organisms*. Proceedings of the 18th European Marine Biology Symposium. University of Oslo, Oslo, Norway.
- Piepenburg, D., A. Brandt, K. von Juterzenka, M. Mayer, K. Schnack, D. Seiler, U. Witte, and M. Spindler. 2001. Patterns and determinants of the distribution and structure of benthic faunal assemblages in the northern North Atlantic. Pages 179–198 in P. Schäfer, W. Ritzrau, M. Schlüter, and J. Thiede, editors. *The northern North Atlantic: a changing environment*. Springer, New York, New York, USA.
- Piepenburg, D., and M. K. Schmid. 1996. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. *Polar Biology* 16:383–392.
- Pierrot, D., E. Lewis, and D. W. R. Wallace. 2006. MS Excel program developed for CO₂ system calculations. ORNL/CDIAC-105. Carbon Dioxide Information Analysis Centre, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.
- Politi, Y., E. Klein, T. Arad, S. Weiner, and L. Addadi. 2004. Sea urchin spine calcite forms via a transient amorphous calcium carbonate phase. *Science* 306:1161–1164.
- Powell, E. N., and D. J. Davies. 1990. When is an “old” shell really “old”? *Journal of Geology* 98:823–844.
- Powell, E. N., R. J. Stanton, D. Davies, and D. A. Logan. 1986. Effect of a large larval settlement and catastrophic mortality on the ecologic record of the community in the death assemblage. *Estuarine, Coastal and Shelf Science* 23:513–525.
- Raz, S., P. C. Hamilton, F. H. Wilt, S. Weiner, and L. Addadi. 2003. The transient phase of amorphous calcium carbonate in sea urchin larval spicules: the involvement of proteins and magnesium ions in its formation and stabilization. *Advanced Functional Materials* 13:480–486.
- Reaves, C. M. 1986. Organic matter metabolizability and calcium carbonate dissolution in nearshore marine muds. *Journal of Sediment Petrology* 56:486–494.
- Rees, H. L., and P. J. Dare. 1993. Sources of mortality and associated life-cycle traits of selected benthic species: a review. Fisheries Research Data Report Number 33. Directorate of Fisheries Research, Lowestoft, UK.
- Rees, S. A., B. N. Opdyke, P. A. Wilson, and T. J. Henstock. 2007. Significance of Halimeda bioherms to the global carbonate budget based on a geological sediment budget for the Northern Great Barrier Reef, Australia. *Coral Reefs* 27:177–188.
- Ricciardi, A., and E. Bourget. 1998. Mass-to-mass conversion factors for marine benthic macroinvertebrates. *Marine Ecology Progress Series* 163:245–251.
- Ridgwell, A., and R. Zeebe. 2005. The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth and Planetary Science Letters* 234:299–315.
- Ries, J. B., D. C. McCorkle, and A. L. Cohen. 2008. Effects of pCO₂-driven reductions in seawater CaCO₃ saturation state on the biomineralization of aragonitic and low-to-high Mg calcitic marine invertebrates and algae. *Eos Transactions AGU, Ocean Sciences Joint Meeting, OS003, Abstract 2884*.
- Ries, J. B., S. M. Stanley, and L. A. Hardie. 2006. Scleractinian corals produce calcite, and grow more slowly, in artificial Cretaceous seawater. *Geology* 34:525–528.
- Rosenberg, R., and L. O. Loo. 1988. Marine eutrophication-induced oxygen deficiency effects on soft bottom fauna, western Sweden. *Ophelia* 29:213–226.
- Rude, P. D., and R. C. Aller. 1991. Fluorine mobility during early diagenesis of carbonate sediment: an indicator of mineral transformations. *Geochimica et Cosmochimica Acta* 55:2491–2509.
- Ruhl, H. A. 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology* 88:1250–1262.
- Russo, A. R. 1980. Bioerosion by two rock boring echinoids, *Echinometra mathaei* and *Echinostrephus aciculatus*, on

- Enewetak Atoll, Marshall Islands. *Journal of Marine Research* 38:99–110.
- Sabine, C. L., R. M. Key, A. Kozyr, R. A. Feely, R. Wanninkhof, F. J. Millero, T. H. Peng, J. L. Bullister, and K. Lee. 2005. ORNL/CDIAC-145, NDP-083. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.
- Sala, E., M. Ribes, B. Hereu, M. Zabala, V. Alva, R. Coma, and J. Garrabou. 1998. Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the north-western Mediterranean: comparison between a marine reserve and an unprotected area. *Marine Ecology Progress Series* 168:135–145.
- Schafer, W. 1972. *Ecology and palaeoecology of marine environments*. University of Chicago Press, Chicago, Illinois, USA.
- Scheibling, R. E., and R. L. Stephenson. 1984. Mass mortalities of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia. *Marine Biology* 78:153–164.
- Schiebel, R. 2002. Planktic foraminiferal sedimentation and the marine calcite budget. *Global Biogeochemical Cycles* 16:13–21.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, London, UK.
- Shin, H. C., and C. H. Koh. 1993. Distribution and abundance of ophiuroids on the continental shelf and slope of the East Sea south-western Sea of Japan, Korea. *Marine Biology* 115:393–399.
- Sloan, N. A., and T. H. Aldridge. 1981. Observations on an aggregation of the starfish *Asterias rubens* in Morecambe Bay, Lancashire, England. *Journal of Natural History* 15:407–418.
- Smith, A. B. 1984. *Echinoid palaeobiology*. George Allen and Unwin, London, UK.
- Smith, C. R., F. C. De Leo, A. F. Bernardino, A. K. Sweetman, and P. Martinez Arbizu. 2008. Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology and Evolution* 23:518–528.
- Smith, C. R., and S. C. Hamilton. 1983. Epibenthic megafauna of a bathyal basin off southern-California: patterns of abundance, biomass, and dispersion. *Deep-Sea Research I* 30:907–928.
- Smith, S. V. 1972. Production of calcium carbonate on the mainland shelf of southern California. *Limnology and Oceanography* 17:28–41.
- Spero, H. J., J. Bijma, D. W. Lea, and B. E. Bemis. 1997. Effect of seawater carbonate ion concentration on foraminiferal carbon and oxygen isotopes. *Nature* 390:497–500.
- Stanley, S. M., J. B. Ries, and L. A. Hardie. 2005. Seawater chemistry and coccolithophore population growth, and the origin of Cretaceous chalk. *Geology* 33:593–596.
- Summers, A. C., and J. Nybakken. 2000. Brittle star distribution patterns and population densities on the continental slope of central California (Echinodermata: Ophiuroidea). *Deep-Sea Research II* 47:1107–1137.
- Tang, C. M., D. J. Bottjer, and M. J. Simms. 2000. Stalked crinoids from a Jurassic tidal deposit in western North America. *Lethaia* 33:46–50.
- Thatje, S., and E. Mutschke. 1999. Distribution of abundance, biomass, production and productivity of macrozoobenthos in the Sub-Antarctic Magellan Province (South America). *Polar Biology* 22:31–37.
- Tokeshi, M. 2002. Spatial distribution of a deep-sea crinoid *Pentametrocrinus tuberculatus* in the Izu-Ogasawara Arc, western Pacific. *Journal of Zoology* 258:291–298.
- Turon, X., G. Giribert, S. López, and C. Palacin. 1995. Growth and population structure of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting habitats. *Marine Ecology Progress Series* 122:193–204.
- Tyrrrell, T., B. Schneider, A. Charalampopoulou, and U. Riebesell. 2008. Coccolithophores and calcite saturation state in the Baltic and Black Seas. *Biogeosciences* 5:485–494.
- Uthicke, S., B. Schaffelke, and M. Byrne. 2009. A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs* 79:3–24.
- Verling, E., D. K. A. Barnes, and A. C. Crook. 2005. Smashing tests? Patterns and mechanisms of adult mortality in a declining echinoid population. *Marine Biology* 147:509–515.
- Vinogradov, A. P. 1953. *The elementary chemical composition of marine organisms*. Sears Foundation for Marine Research, New Haven, Connecticut, USA.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. 11). *Human Biology* 10:181–213.
- Ware, J. R., S. V. Smith, and M. Reaka-Kudla. 1992. Coral reefs: sources or sinks of atmospheric CO₂? *Coral Reefs* 11:127–130.
- Warner, G. F. 1971. On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom* 51:267–282.
- Watson, S. A., P. A. Tyler, and L. S. Peck. 2008. Calcified marine invertebrates: latitudinal variation and ocean acidification. Page 18 in *Effects of Climate Change on the World's Oceans International Symposium*, Gijon, Spain. (<http://www.ocean-acidification.net/Symposium2008/Monaco.Meeting.Book.pdf>)
- Weber, J. N. 1968. Fractionation of the stable isotopes of carbon and oxygen in calcareous invertebrates: the Asteroidea, Ophiuroidea and Crinoidea. *Geochimica et Cosmochimica Acta* 32:33–70.
- Weber, J. N. 1969. The incorporation of magnesium into the skeletal calcites of echinoderms. *American Journal of Science* 267:537–566.
- Westbroek, P., J. R. Young, and K. Linschooten. 1989. Coccolith production (biomineralisation) in the marine alga *Emiliania huxleyi*. *Journal of Protozoology* 36:368–373.
- Wilkinson, B. H. 1979. Biomineralization, paleoceanography, and the evolution of calcareous marine organisms. *Geology* 7:524–527.
- Wilson, R. W., F. J. Millero, J. R. Taylor, P. J. Walsh, V. Christensen, S. Jennings, and M. Grosell. 2009. Contribution of fish to the marine inorganic carbon cycle. *Science* 323:359–362.
- Wollast, R., R. M. Carrels, and F. T. Mackenzie. 1980. Calcite seawater reactions in ocean surface waters. *American Journal of Science* 280:831–848.
- Wood, H. L., J. I. Spicer, and S. Widdicombe. 2008. Ocean acidification may increase calcification rates, but at a cost. *Proceeding of the Royal Society B* 275:1767–1773.
- Zann, L., J. Brodie, C. Berryman, and M. Naqasima. 1987. Recruitment, ecology, growth and behavior of juvenile *Acanthaster planci* (Echinodermata: Asteroidea). *Bulletin of Marine Science* 41:561–575.
- Ziveri, P., A. C. Broerse, J. E. Hinte, and S. Honjo. 2000. The fate of coccoliths at 48°N 21°W, northeastern Atlantic. Particle flux and its preservation in deep-sea sediments. *Deep-Sea Research II* 47:1853–1875.

APPENDIX

A table showing global echinoderms database details along with the sampling method used to collect samples and to estimate density and biomass, and a figure showing GLODAP bottle data distribution used to estimate the calcite compensation depth ($\Omega = 1$) with depth in Fig. 4 (*Ecological Archives* M080-015-A1).