Biochemical Systematics and Ecology, Vol. 19, No. 5, pp. 347–356, 1991.
Printed in Great Britain.

0305-1978/91 $3.00 + 0.00

Chitin Biomass and Production in the Marine Environment

CHARLES JEUNIAUX and MARIE FRANÇOISE VOSS-FOUCART

Laboratories of Morphology, Systematics and Animal Ecology, University of Liège, 22 quai Van Beneden, B-4020 Liège, Belgium

Key Word Index—Chitin; biogeochemical cycles; biomass; production; marine ecology; marine benthos; marine zooplankton.

Abstract—The total production of chitin has been tentatively calculated on the basis of original analytical data on chitin in zooplankton and in benthic communities growing on experimental substrates studied in the Mediterranean Sea, together with data in the literature dealing with total and exuviae production by krill and by some large crustacean species. It appears that crustaceans are the main chitin producers both in planktonic and benthic ecosystems, and that mean total production of chitin in the whole marine biocycle is at least of 2.3 million metric tons per year.

Introduction

It has often been claimed that chitin is, after cellulose, the most abundant polysaccharide produced by living beings in the biosphere. However, it has always been difficult to give accurate data concerning the amounts of chitin actually produced and accumulated in the different types of ecosystems and, finally, in the biosphere. A correct evaluation of chitin standing biomass and production is, however, the first step in the understanding of the place that chitin takes in biogeochemical cycles of C and N. It is also the main critical parameter for the management of any kind of industrial exploitation of chitin natural resources.

In the present review, we should like to draw up an inventory of the main chitin producers in the marine environment, and to try to compare the chitin biomass and production in some typical marine ecosystems.

Methods for Chitin Identification

Most classical methods for chitin identification lack specificity and their application sometimes leads to contradictory interpretations. This is the case of the so-called chitosan method [1], used successfully by some authors in some favourable cases [2]; its limits of application were discussed by Sundara Rajulu *et al.* [3]. Some physical methods, such as X-ray diffraction [4] and infra-red spectroscopy [5, 6] are quite appropriate to detect chitin in a biological system without ambiguity, but only if chitin is present in sufficient amounts; these methods are, of course, purely qualitative.

The quantitative method of Hackman [7, 8], called "alkaline extraction", is based on the residual weight remaining after removal of all organic and inorganic constituents by several treatments. This method is only appropriate to chitin determination in the case of isolated organisms or skeletal pieces, in which chitin is the unique constituent able to withstand such a procedure of isolation, as for instance in crustaceans.

A more specific method, giving both quantitative and qualitative data, is the enzymatic method, based on the high specificity of purified chitinases and on the measurement of the end products after complete hydrolysis. Chitinases (EC 3.2.1.14) of bacterial origin have been produced and purified by the procedures of Jeuniaux [9–12], Berger and Reynolds [13], Otakara [14, 15] and Skujins *et al.* [16]. Purified chitinases may now be purchased from different commercial firms. The procedure for chitin determination by enzymatic method, used in our analytical studies of chitin biomass and production, is as follows [11, 17]. Dry powdered material was decalcified

in 0.5 N HCl at room temperature, washed and treated by 0.5 N NaOH at 100° for 3–6 h in order to set chitin free from glycoproteic complexes and allow further enzymatic hydrolysis. Incubations in chitinase solutions buffered at pH 5.2 (citric acid–Na_2 HPO_4 0.1 M) at 37° were repeated until complete hydrolysis was achieved. The supernatants, containing products of chitin hydrolysis (mainly chitobiose), were then incubated with *N*-acetylglucosaminidase solution (lobster serum is a suitable and easy to handle source of powerful *N*-acetylglucosaminidase), and the resulting *N*-acetylglucosamine was measured by colorimetry [18].

Results are expressed as chitin in mg g^{-1} of dried starting material or per gram of decalcified organic matter, taking into account a correction factor of 0.92 for the introduction of one H_2O molecule per each hydrolysed glycosidic bond. These values must however be taken as default values, as some acetylglucosamine residues in the chitin chain are replaced by glucosamine residues, in a proportion which can vary with several natural or artefactual factors [19]. When chitin biomass and production are studied, these chitin values are expressed by surface units.

Chitin Biosynthesis and Organization

In all the cases so far studied, in molds and yeasts, in insects and crustaceans, chitin is synthesized by the same system: a chitin-synthase (or chitin UDP-acetyl-glucosaminyltransferase: EC 2.4.1.16) catalyses the transfer of one *N*-acetyl-glucosamine residue on a receptor, probably some kind of chitodextrin, from a nucleotide sugar substrate: UDPAG (uridine-diphosphate-*N*-acetylglucosamine) as donor. Chitin synthase is elaborated in an inactive form of chitin-synthase zymogen, which requires limited proteolysis for its activation.

There is some controversy concerning the ultrastructural aspects of chitin biosynthesis. In the mold *Mucor rouxii*, it seems that the synthesis takes place at the level of "chitosomes", spherical organites of 45–65 nm diameter [20–22]. Despite the questionable observations of Cohen [23] using tissue culture of an insect, *Tenebrio molitor*, such intracellular vesicular organites have never been observed *in situ* in epidermal cells of insects or crustaceans during the active phase of chitin synthesis and deposition which takes place at every molting period.

Ultrastructural aspects of chitin secretion and deposition have been followed with the electron microscope in some typical animal tissues. In insects, Locke [24, 25] showed that chitin is probably secreted through specialized zones of the apical membrane of epidermal cells, called "dense plaques". Such "dense plaques" are also obvious in the epidermis of crustaceans during molting [26–28].

In Crustaceans, during the periods of molting when the new cuticle is laid down, there is a thin zone outside the epidermis apical membrane, made up of poorly organized chitinous and proteic material, in which thin fibrillar elements may already be detected [27, 28]. A more elaborated organization takes place a few micrometres above, where chitinoproteic microfibrils become obvious, running parallel to the surface of the epidermal membrane.

According to Blackwell and Weih [29], chitin microfibrils in the *Megarhyssa* ovipositor cuticle are made of a central crystalline chitin core, about 2.8 nm thick, containing 18 to 21 chitin molecules running antiparallel, surrounded by a protein sheath. The protein molecules are probably arranged in a helicoïdal sheath around the core, and are probably linked to chitin covalently [30]. These chemical and physical features probably explain why chitin cannot be hydrolysed by chitinase, as long as the proteic constituents of the chitino-proteic complex remain ("free" and "bound" chitin), [31, 32]. Such a chemical association between chitin and protein, and the microfibrillar organization of the chitino-proteic complex seem to be the rule in most animal structures: they have been observed in many different skeletal or cuticular structures. In some cases, such as the crustacean cuticle, the chitino-proteic microfibrils are

associated into macrofibres which also run parallel to the secreting epidermis. Between these fibres, spaces are, in the case of calcified exoskeletons, occupied by $CaCO_3$ deposits.

This highly organized structure of chitinous materials, together with the genuine resistance of chitin to chemicals, explains their mechanical and biochemical performances, and their wide use by invertebrate animals as an organic matrix in most cuticles and exoskeletons. However, let us keep in mind that in animals, chitinous morphological structures are not necessarily built up of bulky anhistous material, devoid of any contact with living tissue. In crustaceans, for instance, it is worth noticing that the chitinous cuticle is perforated by numerous intracuticular canals (from 3×10^5 to 2×10^6 mm^{-2} in *Carcinus maenas* [27, 28]) containing cellular extensions which arise from subjacent epidermis cells. The cellular extensions retract at the end of every molting period, leaving a cuticular material pierced with holes. Such a perforated structure will greatly enhance the invasion by bacteria, molds and hydrolytic enzymes in the dead cuticle or in the exuviae after molting, and thus accelerate the degradation processes [27, 28].

Chitin Producers in Marine Ecosystems

Chitin biosynthesis seems to be a primitive property of the eukaryote cell [33]. While completely lacking in bacteria and blue-green algae, chitin is produced by different types of unicellular eukaryotes such as diatoms [34], yeasts, Rhizopoda [35], Foraminifera [36], Cnidosporidia [37] and Ciliata [38]. Molds and fungi are also well-known chitin producers.

Chitin is widely used in the animal kingdom: the evolutionary tendencies of chitin utilization by animals have been discussed elsewhere [33, 39] and can be summarized briefly as follows. Chitin is produced by most Coelenterates (mainly Hydrozoans) but not by corals, sea anemones, jelly fishes and sponges. Chitin is elaborated by most triblastic invertebrate groups, among which Bryozoans and Brachiopods are of special interest, as they are often abundant in marine benthic communities. Other chitin producing invertebrates are of course molluscs, polychete worms and arthropods. On the other hand, in the phylogenetic lineage which is supposed to lead to vertebrates, chitin synthesis is lacking, with the unique exception of Tunicates, at the level of peritrophic membranes.

All these animal groups may contribute to the production of chitin biomass in marine ecosystems. The contribution of one single animal group or species depends upon its abundance in the ecosystem, and upon the amount of chitin produced by each individual. It must be emphasized that the amount of chitin in a given type of structure and in a given animal group may vary to a wide extent. In Hydrozoa for instance, the chitin content of the perisarc varies from 10 to 30% of the dry weight of organic matter, while in Bryozoa, the chitin proportion varies from 3 to 15% of decalcified dry weight [11, 41]. It thus appears that it would be impossible to get an approximate estimation of chitin biomass in a given marine community, without a direct analysis of chitin *in situ*, in the biological community itself. A few data are now available in some particular cases, and are discussed below.

Chitin Biomass and Production

Chitin production by zooplankton

The biomass and production of chitin by a typically oceanic zooplankton was estimated in the bay of Calvi (Corsica) in the Mediterranean Sea [42, 43]. Plankton was sampled and analysed during two annual cycles. The results were expressed with respect to a square metre of surface water for a water column of 100 m depth. The zooplankton biomass was dominated (more than 90% of the total biomass) by five species of copepods (belonging to the genus *Acartia*, *Calanus*, *Clausocalanus*,

Centropages and *Oïthona*) and by cladocera. The daily production (P) of every species (or group of species) was estimated by the "cumulative growth method" of Winberge [44] adapted for species with several larval instars during the life span:

$$P = \sum_{n=1}^{i} \frac{N\text{n}.\ \Delta\ \overline{W}\text{n}.\text{Cn}}{t\text{n}}$$

where i is the number of successive larval instars up to the adult stage, Nn is the number of individuals of each instar n, tn the duration of instar n, $\Delta\overline{W}$n the total dry weight increment during the instar n, and Cn the chitin proportion in % of the total dry weight of larval instar n.

Chitin proportion was measured by enzymatic method [11, 17] in each dominant species. With respect to dry weight, chitin was found relatively constant during larval development and in adults of a given species, but varied from species to species, ranging from 3.1% in *Clausocalanus* spp. to 8.58% in *Acartia clausi* and reaching 12.2% in the dominant cladoceran *Evadne* spp.

Taking all these values into account, the mean daily chitin production by planktonic crustaceans (copepods, cladocerans and decapod larvae) was calculated. Seasonal variations were found to be very wide, with a maximum of 20 mg m^{-2} day^{-1} in May, which corresponds to a contemporary chitin biomass of 414 mg m^{-2}. Mean annual chitin production was 1.0014 g m^{-2} yr^{-1}, for a mean biomass value of 26.3 mg m^{-2} (Table 1).

It must be pointed out that, in these estimations, exuviae were not taken into account. Thus, the values calculated for chitin production must be considered as default values, although it has been shown that in planktonic copepods, a part of the chitin of the cuticule is hydrolysed and recovered by the molting animal before ecdysis.

Other data on chitin production by plankton are very scarce. However, we may try to estimate chitin production by some other zooplanktonic communities on the basis of analytical values of total weight or exuviae production. In Lake Baïkal, according to the weight of exuviae produced during their larval development by the populations of *Cyclops* and of *Epishura* [45], the total chitin production by these two dominant groups of planktonic crustaceans amounted to 44.17 mg m^{-2} yr^{-1} (a low value, probably

TABLE 1. CHITIN BIOMASS AND PRODUCTION BY MARINE ZOOPLANKTON* AND BY KRILL† (MEAN ANNUAL VALUES)

Communities	Chitin biomass mg m^{-3}	(mg m^{-2})	Chitin production mg m^{-3} yr^{-1}	(mg m^{-2} yr^{-1})	Authors
Krill:			exuviae not included		
Atlantic Ocean and North Sea					[53]
Max.	0.62	(31)	0.85	(42)	
Min.	0.21	(10.5)	0.24	(12)	
			exuviae included		
Krill:					
Nyctiphanes australis Storm Bay, Australia					[54]
Mean values	0.416	(20.08)	21.47	(1077)	
			exuviae not included		
Surface zooplankton					
(copepods + cladocerans)					[43]
Calvi Bay, Corsica					
Mean values	26.3			1001.4	
Max.	(414)			20mg m^{-2} day^{-1}	

*Measured by enzymatic method. †Calculated on the basis of Yanase [52] data for *Euphausia superba* (chitin = 7.08% whole body dry weight = 38.7% cuticle dry weight).

explained by the cold climate of central Siberia and by the fact that the other planktonic species, though less important, were not taken into account). In eutrophic lakes of northern atlantic Europe, the zooplankton of which is mainly made up of "water flies" (cladocerans) of the genus *Daphnia*, the calculated production of chitin amounted to 136–302 mg m^{-2} yr^{-1} in Lake Tjeukemeer in Holland [46] and to 3200 mg m^{-2} yr^{-1} in Lake Esrom in Denmark [47]. These values are of the same order of magnitude as those obtained for marine zooplankton of the Mediterranean Sea.

Chitin production by krill

The part played by krill (Euphausiids) in the production of chitin must certainly be examined carefully in the present review, as krill are one of the most important components of the marine pelagic food web. Recent estimates of annual production of antarctic krill varied from 16 to 1250 million tons per year [48] or, more likely, from 100 to 500 million metric tons (wet weight) per year [49]. Krill fisheries have operated since 1960 for the commercial utilization of the edible tail [50, 51]. These estimations, however, were not founded on direct analysis of population densities, but rather on indirect indications. We can try to get estimations of chitin production by krill, using results of exhaustive studies of krill populations in the North Atlantic or South Pacific oceans. In both cases, we translate the values of total krill biomass and production in terms of chitin biomass and production, assuming that the chitin proportions obtained by Yanase [52] for *Euphausia superba* are representative of other Euphausiid species (7.08% of total dry weight, and 38.7% of dried cuticle).

Calculated from the data of Lindley [53], chitin biomass of krill would be highest in the Norwegian Sea (0.62 mg m^{-3}) and principally originated from the species *Meganyctiphanes norvegicus*. In other parts of the North Sea and North Atlantic Ocean, chitin biomass varies from 0.21 to 0.37 mg m^{-3}, the dominant species being different from one region to another. Chitin production values thus range from 0.24 to 0.28 mg m^{-3} yr^{-1} in most ocean areas, to more than 0.85 mg m^{-3} yr^{-1} in the Norwegian Sea, North Sea, Nova Scotia and Iberia Shelf (Table 1). These values were obtained for populations taken by continuous towing at a 10-m depth. If we take into account the scattered vertical distribution* of krill "swarms", chitin biomass and production in a water column of 100 m depth would vary respectively from 10.5 to 31 mg m^{-2} (biomass) and from 12 to 42 mg m^{-2} yr^{-1} (production). This seems to be considerably lower than the values obtained for zooplankton but, as far as chitin production is concerned, these calculated values for krill are probably far less than the actual ones, if we remember that the production of exuviae has not been taken into account!

The data published by Ritz and Hosie [54] on a krill community in the South Pacific near the Australian coasts, dominated by *Nyctiphanes australis*, are more useful for our purpose as they include the production of exuviae. For a mean annual chitin biomass of 416 mg m^{-3}, the total chitin production by exuviae was estimated to be 15.87 mg m^{-3} yr^{-1}, or, if we extrapolate for a water column of 100 m depth, a chitin biomass of 20 mg m^{-2} and a chitin production of about 800 mg m^{-2} yr^{-1}. The total chitin production by adults may be estimated to be 5.6 mg m^{-3} yr^{-1}, or 283 mg m^{-2} yr^{-1}. Thus, the total chitin production (adults + exuviae) would be 1.077 g m^{-2} yr^{-1} (Table 1). The latter figure is much higher than that calculated from Lindley's values for a similar biomass, and is very close to the value of 1.0014 g m^{-2} yr^{-1} obtained for copepods and cladocerans of a mediterranean zooplankton (Table 1).

*It may be assumed that krill swarms generally occupy only half of the water column, due to their scattered distribution [55].

Chitin biomass and chitin production by marine benthic communities

The biomass and production of chitin by benthic communities growing on rocky substrates has been studied in a single, relatively well delimited marine area, namely the Bay of Calvi on the Isle Corsica (Mediterranean Sea). In infralittoral communities of photophilous algae, characterized by several species of *Cystoseira*, the chitin biomass was principally due to sessile and incrusted colonies of Bryozoa and Hydrozoa, on one hand, and to vagile and crawling species of crustaceans on the other. The whole benthic biological cover, including small species of decapod crustaceans, contributed to a mean chitin biomass of 1.11 g m^{-2}. In sciaphilous communities inhabiting semi-dark caves, the chitin biomass due to incrusting colonies of Hydrozoans and Bryozoans was lower, but the contribution of decapod crustaceans, while highly variable, was sometimes very important. The mean chitin biomass value was tentatively estimated to 1.4 g m^{-2} [56].

The rate of chitin production by infralittoral communities living on rocky shores was estimated by measuring the amount of chitin accumulated after given periods of time by pioneering communities allowed to settle and to grow on naked substrates assuming that, in this case, predation and mortality are negligible. Several sets of rectangular plates of granite, baked clay, glass and PVC were immersed at different depths (from 6 to 37 m) and kept in natural conditions. At given intervals, sets of plates were removed, and the whole biological cover was scraped, dried, weighed and powdered by mechanical grinding. The powder was used for chitin determination by enzymatic method and the results calculated per square metre. We verified that the species composition of the biological cover on the plates was, after a few months, roughly similar to that of neighbouring benthic communities. The results [57, 58] showed that during the first year, the development of pioneering communities was relatively similar on the different types of substrates studied, except on glass on which it was lower. The production was low during the first year, then quicker during the second year, at least at 18 m depth. Chitin production was estimated to about 0.30 g m^{-2} yr^{-1} during the first year, and to 1 g m^{-2} yr^{-1} during the second year, when it was likely that the benthic community had reached a climax. Chitin production seemed to be lower at a depth of 37 m, as well as inside a Posidonia meadow, at 18 m depth, probably due to the concurrence of Posidonia leaves as substrate for the settlement of larvae [57, 58].

We were interested to find if the production of chitin by pioneering benthic communities was significantly different on different kinds of artificial plastic substrates. Using the same method of naked immerged plates in the mediterranean bay of Calvi, we were able to analyse the chitin biomass produced by benthic communities growing on six different plastic matters: plexiglass, polyethylene, nylon, polystyrene, polycarbonate and PVC. The results (Table 2) [59] showed that chitin production, calculated

TABLE 2. CHITIN PRODUCTION BY PIONEERING BENTHIC COMMUNITIES GROWING ON NAKED PLASTIC PLATES AT 37 M DEPTH, IN THE MEDITERRANEAN SEA (CORSICA), FROM AUGUST TO MARCH 1989 [59]

Plastic nature	Chitin biomass (mg m^{-2})*		Calculated† chitin production (mg m^{-2} $year^{-1}$)
	after three months	after seven months	
Plexiglass	27	184	315
Polyethylene	38	213	365
Nylon	51	349	598
Polystyrene	25	376	644
Polycarbonate	22	188	322
PVC	13	436	747

*Mean values of five different plates (10×20 cm). †Assuming that the rate of chitin production in the community during the first seven months will remain constant during the next five months of the first year.

on the first seven months and extrapolated, varied between 315 and 745 mg m^{-2} yr^{-1}. Such values are only slightly lower than those obtained with granite and baked clay as substrates, on which chitin production amounted to 1 g m^{-2} yr^{-1} [57, 58].

Chitin production by some natural populations of large crustacean species

We have already noted that crustaceans are the main chitin producers in infralittoral benthic communities growing on rocky substrates. However, in these experiments, large decapod species inhabiting crevices, such as lobsters and crabs, were not taken into account. The importance of these crustaceans as chitin producers is obvious, owing to the part occupied by crabs and lobsters in fisheries and canning industries. Some authors [60] estimated 39,000 tons the amount of chitin available yearly as wastes of fisheries. However, specific productivity studies of natural populations are scarce.

We have calculated the annual production of chitin in a population of lobsters on the basis of the exhaustive data published by Berry and Smale [61] and dealing with a natural population of the spiny lobster *Panulirus homarus* inhabiting a small isolated reef of the Natal Coast in South Africa. Taking into account the production of fresh tissue, cuticle and cast skins (exuviae), and their respective content of chitin, the chitin production was estimated to 1.5 g m^{-2} yr^{-1}. Such a figure concerning a single species is of the same order of magnitude as the values of chitin production obtained so far for the whole pioneering benthic communities growing on naked substrates! In the case of other large decapod species in other ecosystems, the production by a mature population of the crayfish *Astacus astacus* in Lake Biajourkas (Lithuania) was only 0.079 g m^{-2} yr^{-1} (calculated from Tsoukerzis *et al.* [62]).

Discussion and Conclusions

The few data so far available on chitin productivity, which have been discussed in the present review, are summarized in Table 3, where the values are given in grams of

TABLE 3. CHITIN PRODUCTION BY SOME NATURAL COMMUNITIES

Community	Annual chitin production (g m^{-2} $year^{-1}$)	Authors
Sea water		
Krill, Australia	1.077	[54]
Surface zooplankton (copepods—cladocerans) (Calvi Bay, Mediterranean Sea)	1.0014	[43]
Pioneering benthic communities (Calvi Bay, Mediterranean Sea)		
Depth: 18 m	(first year) 0.30	
	(second year) 1.00	[58]
37m	(first year) 0.23	
	(second year) 0.17	
Spiny lobster population (Natal coasts)	1.5*	[61]
Fresh water		
Arthropods, eutrophic lake, Japan	51.0	[63]
Plankton (*Daphnia*) eutrophic lakes		
—Holland	0.13–0.30*	[46]
—Denmark	3.2*	[47]
Bryozoans (*Plumatella*) River, Belgium	21.0*	[64]

*Values calculated from total dry weight production, exuviae included.

chitin produced per year per square metre of surface water (for a water column of 100 m depth) in the case of krill and plankton, or per square metre of rocky surface in the case of benthic communities and lobster populations. It may be seen that secondary chitin production is of the same order of magnitude (around 1 g m^{-2} yr^{-1}) in the main marine biological communities so far considered, if expressed by square metre. Such values of chitin production are roughly similar to those obtained in some typical freshwater habitats, such as eutrophic baltic lakes in Europe, but they are much lower than those obtained for a freshwater arthropod community in an organopolluted lake in Japan [63] or for freshwater moss-animals (Bryozoans) observed in a polluted river in Belgium [64].

We may try, tentatively, to evaluate the total chitin production in the whole marine biocycle, on the basis of the values given in Table 3, taking into account the estimations of surface occupied by the main marine habitats given by Milliman [65] and Tchernia [66]. The calculated values of total chitin production in marine ecosystems are shown in Table 4; they have been calculated assuming the following considerations. On one hand, chitin production by krill was extrapolated for a water column of 500 m depth, according to the vertical distribution of larvae and adults, while chitin production by zooplankton was calculated for the euphotic pelagic layer, i.e. 100 m depth. On the other hand, chitin production by large decapod crustacean species (crabs, lobsters) was calculated on the basis of data of Berry and Smile [61] for the unique spiny lobster, with a correction factor of ×4, assuming that a given rocky habitat in a eulittoral zone does not generally harbour more than four different dominant species of this group.

Assuming these postulates, the total chitin production in the whole marine biocycle would be 2.3 million metric tons per year. This calculated value is surely lower than the actual one, for several reasons: the calculated figures are based on analytical default values; moreover, important chitin producers have not been taken into account, such as shrimps, deep sea prawns, and large crab species living on sandy bottoms. Some other data, indeed, indicate that chitin marine production is probably higher. For instance, the estimations of krill production made by some authors [49] would suggest that krill chitin production could amount to 10–70 g m^{-2} of ocean surface. As far as large crustacean species are concerned, "optimistic" estimates reported by Allan *et al.* [60], based on shellfish fisheries statistics, would amount to a maximum of 39,000 tons of chitin per year (instead of 8400 tons in our evaluation).

However, the calculated chitin production shown in Table 4, even if underestimated, should give a satisfactory idea of the importance of chitin in biogeochemical cycles of

TABLE 4. CHITIN ANNUAL PRODUCTION IN MARINE ECOSYSTEMS

Ecosystem	Extent $\times 10^6$ km^2	Community	Chitin production	Total chitin production (Tons yr^{-1})
Pelagic	360.0	Surface zooplankton*	1.0	360,000
		Krill†	5.3	1,938,000
		Shrimps	?	?
Benthic				
Rocky shores	1.4	Benthic sessile and vagile biological cover	1.0	1400
(0–200m)		Large decapod species‡	6.0	8400
Continental slope	30.6	?	?	?
Sediments	320.0	Limicolous communities	?	?
		Large crab species		
Total				2,307,800

*For a water column of 100 m depth. †For a water column of 500 m depth. ‡Assuming the presence of four dominant large species with a chitin production similar to that of spiny lobster (1.5 g m^{-2} yr^{-1}).

carbon and nitrogen. These quantitative estimations lead us to conclude that these enormous amounts of chitin produced every year in seas and oceans have to be balanced by efficacious biodegradation mechanisms, on pain of considerable immobilization of organic carbon and nitrogen.

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