

Chapter 7

Seamount benthos

Sarah Samadi, Thomas Schlacher and Bertrand Richer de Forges

Abstract

Seamounts are unique habitats for the deep-sea megabenthos. Several distinctive environmental conditions, such as limited spatial extent, geographic isolation, swift currents, localized upwelling and circulation cells create environments favourable for the establishment of diverse benthic assemblages. Relatively large suspension feeders such as corals, sponges and crinoids, can dominate the biomass of these assemblages and form structural habitat for a diversity of smaller, mobile species. The benthos contains species with apparently limited geographic distributions (endemics) and archaic species thought to have become extinct ('living fossils'). Seamounts rise well above the ocean floor and thus form relatively shallow habitat available for bathyal species above the surrounding abyssal seafloor. Growth of seamount invertebrates can be extraordinarily slow and they often have very long life spans. These life-history traits make the seamount benthos highly vulnerable to destructive bottom trawling. The prominence of suspension feeders suggests a simple trophic web, but in fact, benthic food webs are complex: food-chain lengths and trophic architecture rival other marine ecosystems in both shallow and deep settings. The geographic isolation of seamounts has frequently been likened to oceanic islands, where species differences among seamounts can be very high. Yet, seamount populations may not necessarily be genetically isolated if they produce larvae capable of long-distance dispersal. The fauna of seamounts is poorly documented, and the structure of whole assemblages is known from only a limited number of seamounts worldwide, partly as a consequence of dwindling resources and expertise in taxonomy. Lack of basic ecological knowledge impedes the development of global, integrated structural and functional frameworks concerning seamount benthos.

Introduction

Three factors combine to make a comprehensive global synthesis of seamount benthos difficult: (1) Seamounts occur from the tropics to the poles, resulting in a wide ambit of physico-chemical conditions and differences in rates of primary production and food supply to benthic consumers and since communities respond to such environmental variability, the benthos of seamounts is likely to be geographically diverse. (2) Seamounts cover a broad

depth range, including both shallow mounts that extend into the euphotic zone as well as mounts that lie in the bathyal and abyssal zones; as seamount benthos is strongly structured by depth, such wide bathymetric ranges result in a multitude of community types. (3) Seamounts have diverse geological histories and geological ages. Most seamounts are of volcanic origin with basaltic rocks, but guyots (see Chapter 1) can be common in the tropics. Since both substratum type and habitat age influence species composition, the structure of seamount benthos will reflect this diversity.

Theoretically it is possible to envisage faunal surveys that encompass this diversity of geo-morphological types, latitudinal and depth ranges and seamount ages but the reality is starkly different. Of the estimated 100 000 seamounts worldwide (see Chapters 1 and 2), only 232 have been biologically sampled (SeamountsOnline, 2006), and for these very few data on invertebrates are available. In fact, much of our current knowledge on the seamount benthos is a by-product of fisheries studies. A global dearth in taxonomical expertise and resources impedes accurate assessments of benthic diversity, with few surveys identifying the complete spectrum of specimens collected, so that the reported number of seamount species is likely to be a gross underestimate of the total. For example, Wilson and Kaufmann (1987) present a global inventory of the fauna collected on about 100 seamounts that comprises 597 species, many of which are unidentified. Five seamounts account for 72% of the species recorded (Smith and Jordan, 1988; Rogers, 1994), further emphasizing the limited sampling range available for biodiversity assessments of seamounts. Several Russian cruises to the Eastern Pacific (Kuznekov and Mironov, 1981; Parin *et al.*, 1997) yielded 192 reported species, many unidentified, from 25 seamounts. Koslow and Gowlett-Holmes (1998) list 242 invertebrate species from 14 seamounts off Tasmania. By contrast, 730 species have been described from 18 seamounts in New Caledonia (Richer de Forges *et al.*, 2000, 2005). While this is a substantially higher estimate of the benthic species richness at seamounts, it is an underestimate of the true seamount species richness because a large part of the catch awaits taxonomic description.

Because of such limitations in published seamount data, this chapter draws mostly on more recent findings from seamount studies in New Caledonia (south west Pacific) to illustrate several key biological aspects of seamount benthos. We highlight six fundamental ecological properties of the seamount benthos which are likely to be conceptually applicable to other seamount systems worldwide; these include: (1) composition of the benthos; (2) species richness and 'new species'; (3) geographic patterns in species composition (beta-diversity); (4) endemism and genetic structures of benthic invertebrate populations; (5) growth rates, longevity and evolutionary ages of benthic invertebrates; and (6) trophic organization of seamount benthos.

Composition of the benthos

Suspension feeders usually dominate the biomass of the megabenthos on seamounts. Currents are amplified around seamounts (see Chapters 4 and 5), and this is thought to be the principal factor that favours suspension feeders. Taxonomic composition varies between seamounts: assemblages may be dominated by sponges and/or corals like stylasterids or gorgonians. These large suspension feeders provide important habitat for smaller,

mobile invertebrates, with molluscs, crustaceans and echinoderms being particularly species-rich amongst this vagile fauna (Tables 7.1–7.3). For example, stylasterine corals are well represented in the bathyal zone of New Caledonia. High species diversity has been found on hard bottoms south of New Caledonia island, particularly on Norfolk Ridge seamounts (Richer de Forges *et al.*, 1987). About 49 species, of which 26 are new to science, were collected here (Lindner and Cairns, Personal communication).

Table 7.1 Species richness, and the discovery of species new to science, in expeditions to the bathyal region of New Caledonia (Richer de Forges *et al.* 2005). See supplemental material for expedition details.

Higher taxon	Families	Genera	Species	New species	New %
Porifera	61	135	216	142	65.7
Cnidaria	9	19	73	56	76.7
Brachiopoda	14	20	26	5	19.2
Annelida and Sipuncula	6	11	17	7	41.1
Bryozoa	57	122	206	115	55.8
Mollusca	80	245	710	461	64.9
Pycnogonida	8	23	60	37	61.7
Crustacea	98	298	691	362	52.3
Echinodermata	15	30	36	16	44.4
Tunicata	12	36	66	48	72.7
Vertebrata	109	242	414	73	17.6
Total	469	1181	2515	1322	52.5

Table 7.2 Species richness on the seamounts of Norfolk Ridge and Lord Howe Rise (Richer de Forges *et al.* 2005).

Higher taxon	Families	Genera	Species	New species	New %
Porifera	18	26	34	26	76.4
Cnidaria	3	8	19	15	78.9
Brachiopoda	9	11	13	3	23
Annelida and Sipuncula	2	2	2	2	100
Bryozoa	28	44	56	36	64.2
Mollusca	43	96	201	127	63.1
Pycnogonida	4	9	13	8	61.5
Crustacea	49	118	251	163	64.9
Echinodermata	4	6	8	6	75
Tunicata	7	8	9	6	66.6
Vertebrata	54	94	124	19	15.3
Total	223	423	730	411	56.3

Only broad estimates of the distribution of benthic species richness among trophic guilds can be made from published species lists. Wilson and Kaufmann's (1987) global compilation of benthic seamount species indicates that suspension feeders comprise about 52%. But regional datasets provide much lower figures 15% in the Eastern Pacific from several Russian cruises (Kuznetsov and Mironov, 1981; Parin *et al.*, 1997); about 27% on Tasmanian seamounts (Koslow and Gowlett-Holmes, 1998); about 22% on the Lord Howe and Norfolk Ridge in the SW Pacific (Fig. 7.1; Richer de Forges, Personal

Table 7.3 Species richness of the fauna living on the seamounts only.

Higher taxon	Families	Genera	Species	New species	New %
Porifera	6	8	8	5	62.5
Cnidaria	2	4	4	4	100
Brachiopoda	2	2	2	1	50
Annelida and Sipuncula	0	0	0	0	0
Bryozoa	22	29	35	25	71.4
Mollusca	20	39	55	44	80
Pycnogonida	2	4	5	2	40
Crustacea	22	32	42	30	71.4
Echinodermata	2	3	3	3	100
Tunicata	2	3	3	2	66.6
Vertebrata	24	35	39	9	23
Total	104	159	196	125	63.7

communication). While forming the bulk of the biomass, suspension feeders may not necessarily constitute the largest proportion of species in seamount benthos. Their apparent high biomass has, however, not been reported quantitatively for entire assemblages in the published literature, and their abundance is mostly based on qualitative assessments of catches and underwater imagery.

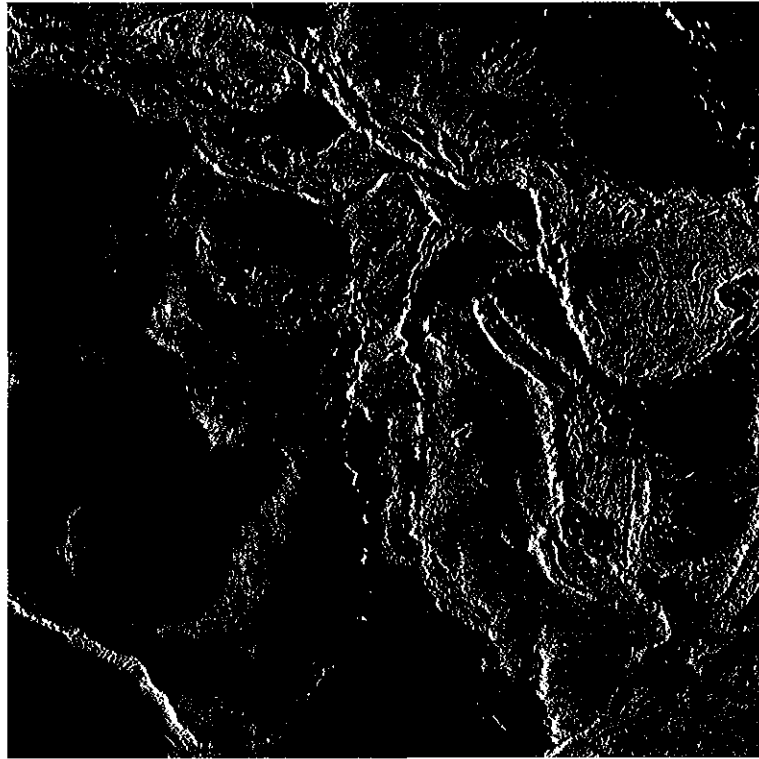


Fig. 7.1 Southwest Pacific map showing ridges, trenches and several seamount lineaments: A: Norfolk Ridge seamounts; B: Lord Howe Rise seamounts; C: Tasmanian seamounts. *Source:* From satellite altimetric mapping NOAA.

Geographic variation in species richness and composition

Several aspects of species richness and geographic variation in community composition are well illustrated by seamount studies in the southwest Pacific (Richer de Forges *et al.*, 2000) based on taxonomically comprehensive collections of megabenthos from three seamount groups: (1) Norfolk Ridge (6 seamounts, 295 samples, 516 species); (2) Lord Howe Ridge (4 seamounts, 35 samples, 108 species) and (3) south of Tasmania (14 seamounts, 34 samples, 297 species).

Estimates of benthic species richness on seamounts can be strongly influenced by collecting effort. Much of the variation in species richness between seamounts in the Coral Sea can be explained by differences in sampling effort (Fig. 7.2). Species richness of

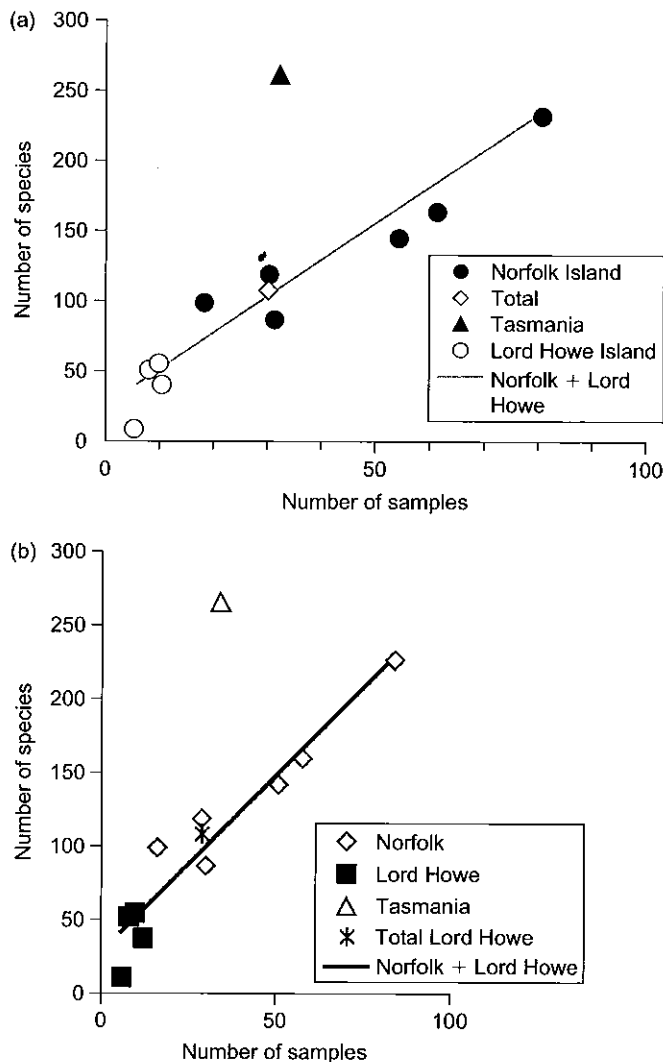


Fig. 7.2 Relationship between number of species and number of samples on the Tasmanian and Coral Sea seamounts. Tasmanian seamounts appear to be richer in species. Source: After Richer de Forges *et al.* (2000).

New %

62.5
100
50
0
71.4
80
40
71.4
100
66.6
23
63.7

may not nec-
essarily appear
larger in the
assessments of

Norfolk Ridge
metric mapping

Tasmanian seamounts appears to be higher, but it is unclear whether this is due to more speciose assemblages, is an artefact of aggregating samples over several seamounts, or results from a positive bias from sampling over a greater depth range.

On SW Pacific seamounts, community composition differed significantly between two ridge systems at similar latitudes separated by about 1000 km (Fig. 7.3; Richer de Forges *et al.*, 2000). Over larger spatial scales (~3000 km) corresponding to a 20° difference in latitude, a completely different set of species was observed between deeper Tasmanian seamounts and the shallower seamounts near New Caledonia: indeed, just four benthic invertebrate species from Tasmanian seamounts are known from the seafloor around New Caledonia.

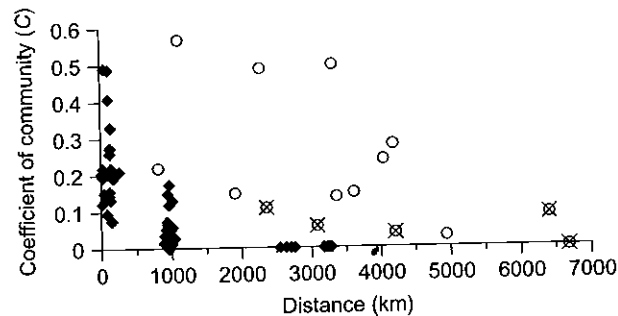


Fig. 7.3 Relationships between the seamounts, distant from each other only by 10 km, and the community coefficient (C) between seamount sites (solid diamond), hydrothermal vents sites from the Eastern Pacific Rise in the North and South Pacific and Galapagos Rift (open circles), and vent sites from disconnected ridges in the north-east Pacific at 41–49°N (crossed circles). Source: After Richer de Forges *et al.* (2000).

The isolation of seamount faunas between the southern and northern Tasman Sea contrasts markedly with the generally strong affinity displayed by the soft-sediment slope fauna between these two regions. This limited dispersal of seamount species is due to the generally small size of seamounts, the considerable distance between them and their unique oceanographic environment (see Chapter 14; Johannesson, 1988; Parker and Tunnicliffe, 1994; Richer de Forges, 2001). Seamounts situated in clusters or along ridge systems may also function as 'island groups' or 'chains' (see Chapters 1 and 4) leading to observed localized species distributions that could encourage speciation between localities.

Endemism

A frequently cited trait of seamount biota is the high level of endemism. Wilson and Kaufmann (1987) estimated that 12–22% of fishes and 15–36% of invertebrates are endemic to seamounts. Accordingly, in the SW Pacific, 36% of species from the Norfolk Ridge seamounts were new to science and not known from sampling of the open seafloor, and are therefore potential endemic species, along with 31% of species from the Lord Howe seamounts and 16–33% of species from Tasmanian seamounts (Richer de Forges *et al.*,

2000). Similarly, 17 new genera were obtained from the Norfolk Ridge samples, 4 from the Lord Howe Ridge and 7–8 from Tasmanian samples (Richer de Forges *et al.*, 2000). Some species appear to be relicts of groups earlier believed to have become extinct in the Mesozoic (Amèziane-Cominardi *et al.*, 1987; Laurin, 1992; Vacelet *et al.*, 1992).

These figures suggest that the level of endemism may be appreciable on seamounts. However, there are few comprehensive assessments of endemism rates available for other marine habitats, and it is thus difficult to judge. The spatial scale over which endemism is defined and reported is a further complication. Essentially, endemism is defined as 'limited geographic range size' of a species, but what this means depends on the spatial scale over which it is defined. At the smallest scale, it can represent a single site on a seamount, a single seamount, seamounts on a single ridge system and seamounts in sub-ocean basins or whole ocean basins. There are also no unambiguous biological criteria for an ecologically meaningful scale over which endemism is measured, save perhaps for populations showing clear genetic isolation. Hence endemism always needs to be qualified by the spatial scale to which it refers.

The rate at which new species were discovered during the exploration of New Caledonia seamounts was high and constant, so we may have overestimated endemism. In their study of the species richness of molluscs in shallow waters off New Caledonia, Bouchet *et al.* (2002) demonstrate that the true number of species was underestimated in the tropical Indo-Pacific. This conclusion could be extrapolated to other ocean habitats.

Among the organisms found on the seamounts of the Norfolk Ridge, squat lobsters (Galatheididae) are very diverse (e.g., Macpherson and Machordom, 2005). In New Caledonia, many species of galatheids have been described from seamounts, but none is endemic to them or to the local ridge of seamounts (Samadi *et al.*, 2006), and, indeed, all species are also found on nearby island slopes. However, species richness is lower along the continental slope than in any seamount along the Norfolk Ridge (see supplemental information at www.seamountsbook.info) suggesting that the Norfolk seamounts is a diversity hotspot for the family Galatheididae, but not an area of endemism. Other studies have also suggested that seamounts, like other prominent topographic features such as reef islands or shelf breaks, are biodiversity hotspots (see for example Worm *et al.* (2003) for vertebrate predators and Heinz *et al.* (2004) for foraminifera). However, our results suggest that while squat lobsters do not exhibit elevated rates of endemism, seamounts are highly productive zones where many species occur at high abundance. This finding is in accordance with the suggestion that high productivity is a prominent ecological feature of seamounts (see Chapters 5 and 14; Fock *et al.*, 2002; Genin, 2004).

Variability of species richness with depth

On the shallowest seamounts, stalked crinoids (*Metacrinus levii*) are found at a depth of 250–300 m, together with dense assemblages of lithistid sponges and stylasterid corals. On the upper parts of these seamounts species richness and biomass are high. Here, sessile suspension feeders dominate the communities and a species-rich assemblages of mobile invertebrates such as crustaceans, molluscs, echinoderms and sometimes brachiopods are present (Richer de Forges *et al.*, 2005).

On the northern part of the Norfolk Ridge, the seamounts are guyots (Fig. 7.4) with flat summits between 230 and 720 m deep. There are few marine geological studies on these features in the SW Pacific (see Van de Beuque, 1999; Veevers, 2000, 2001), but considering their shape and limestone caps, the summits of these seamounts were historically close to or above the sea surface. The bottom of the deeper (>720 m) seamounts is covered with polymetallic crust, with Fe–Mn layers ranging in thickness from a few millimetres to several centimetres, engulfing other dead objects on the seafloor such as fish otoliths and whale bones (see Chapter 1). The rate of deposition of these crusts is estimated to be 1–5 mm year on Hawaiian seamounts (Verlaan, 1992). Where the seafloor is totally covered by manganese crusts, few invertebrates are able to settle, except for sparse gorgonians, sponges and stalked crinoids (Grigg *et al.*, 1987).

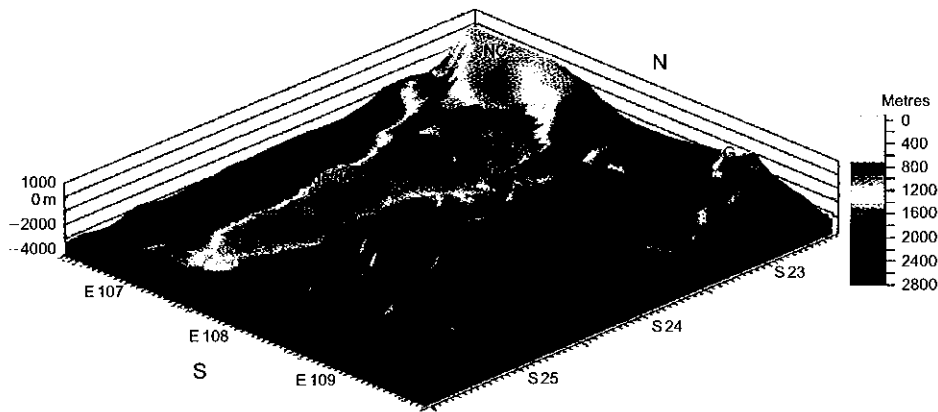


Fig. 7.4 3D view of the south of New Caledonia (NC) showing the relative positions of the main Norfolk Ridge seamounts. M: Munida seamount; Az: Antigonina seamount; St: Stylaster seamount; JO: Jumeau ouest seamount; Je: Jumeau est seamount; A: Kaimon maru seamount; B: Eponge seamount; C: Introuvable seamount.

Seamounts with a summit around 300–600 m host communities of sponges (lithistids and hexactinellids) and stylasterid corals. Species replacement rates in sponges increase with increasing depth separation of sites irrespective of their geographic distance and biological richness declines with depth across several taxonomic levels from species and genera to families; there were between 6 and 47 species of sponges per seamount. Depth appears to be the dominant factor in controlling community composition (Schlacher-Hoenlinger *et al.*, 2005).

‘Living fossils’: sponges, crinoids, brachiopods

Several archaic species or ‘living fossils’ have been discovered on seamounts (Lévi, 1991; Vacelet *et al.*, 1992; Kelly, 2000) especially in New Caledonia, where sampling of seamounts is much higher than anywhere else. A new species of Glypheid has recently been described from a seamount of the Coral Sea (Richer de Forges, 2006). Here we

briefly review the principal groups for which archaic forms have been described from seamounts.

Sponges

Sponges are especially species-rich on shallow seamounts 200–700 m deep (Bouchet and Metivier, 1982; Lévi, 1991). Sixty-one families with 135 genera and 216 species have been recorded in New Caledonia of which 142 species were new (Table 7.1). This sponge fauna, practically unknown before 1977, was principally studied by Lévi (1991, 1993). Its key attributes include: (a) a high species diversity and a change in species at 700 m depth; (b) lithistids and tetractinellids dominate on the upper parts of seamounts; (c) two-thirds of species were new and thus potential endemics, while several genera were previously unknown from the Pacific Ocean; (d) the high diversity of lithistids is comparable only with the fossils from the Cretaceous in Europe. The sponge fauna has strong affinities with Mesozoic fauna, could be derived from the Tethysian mesogea (Lévi, 1991), and may therefore be considered a 'refuge habitat' for relic fauna such as lithistids that appear to be restricted to caves, continental margins and seamounts (Richer de Forges, 2001). Several relic genera from the Norfolk Ridge seamounts, *Neopelta*, *Aulaxinia*, *Neosiphonia* and *Reidispongia* are also known from the northern part of New Zealand (Kelly, 2000).

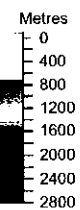
Crinoids

Numerous species of crinoids have been described from the bathyal zone of New Caledonia. Stalked crinoids comprise 9 families, 14 genera and 15 species, with 2 new genera and 8 new species. A large proportion of crinoids is considered to be 'living fossils', with affinities to the Jurassic and Cretaceous fauna from the mesogean Tethys Sea (Amèziane-Cominardi *et al.*, 1987, 1990; Bourseau *et al.*, 1991). The description of this crinoid fauna has totally modified the knowledge of this group for the Indo-Pacific (Bourseau *et al.*, 1991). Fourteen genera are represented (*Metacrinus*, *Saracrinus*, *Diplocrinus*, *Proisocrinus*, *Caledonicrinus*, *Porphyrocrinus*, *Naumachocrinus*, *Bathycrinus*, *Gymnocrinus*, *Holopus*, *Proeudesicrinus*, *Thalassocrinus*, *Hyocrinus*, *Guillecrinus*) and eight species were new. The majority of crinoid genera are true 'living fossils' since they appeared in the fossil record before the great Cretaceous 'crisis' (Lawton and May, 1995). Spectacular examples of these old forms include two species (*Gymnocrinus richeri* and *Holopus alidis*) from the very archaic Hemicrinidae (Fig. 7.5), which have a short and strongly calcified stalk, an adaptation to the strong currents on seamounts (Hess *et al.*, 1999). Cohen *et al.* (2004) proposed a new molecular phylogeny of this group based mainly on material collected from seamounts.

Brachiopods

Laurin (1997) recorded 14 families of Brachiopods, including 19 genera and 26 species of which 4 were new, from the bathyal zone of New Caledonia, mainly from the seamounts: a new genus and a species, *Neoancistrocrania norfolki*, was similar to Cretaceous species (Cohen *et al.*, 1998; Laurin, 1992).

with flat
on these
consider-
ly close
red with
s to sev-
nd whale
1–5 mm
covered
gonians,



Norfolk Ridge
seamount;

lithistids
increase
ance and
species and
nt. Depth
chlacher-

ts (Lévi,
ampling of
recently
Here we

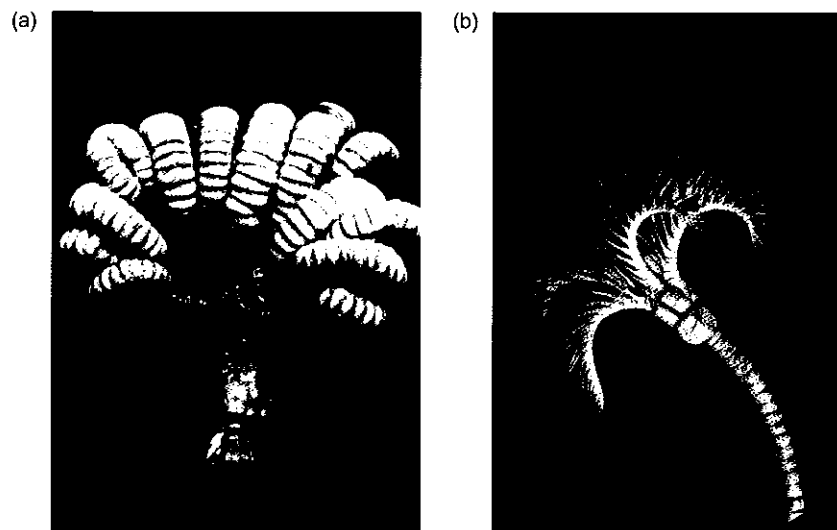


Fig. 7.5 Examples of relic fauna from seamounts: (a) *Gymnocrinus richeri*, from Stylander seamount, 500 m and (b) *Caledonicrinus vaubani*, from Antigonion seamount, 300 m.

Long-lived animals: sponges, octocorals, crinoids

Deep-sea animals have adapted their growth in response to the environmental conditions of darkness, low temperatures and low food availability. The age of individuals can be determined from skeletal material. Here we discuss estimates of growth and age for some benthic invertebrates from seamounts.

Growth of a calcareous sponge (*Vaceletia* sp.) collected from seamounts was determined at 11 mm per century (Vacelet *et al.*, 1991). Most demosponges contain distinct internal silicious skeletal material, with some species producing extraordinary long glass spicules (Beaulieu, 2001). A specimen of the genus *Monoraphis* collected from the seamounts was estimated to be 440 years old based on an analysis of growth rings in its 3.4 m long spicule (Ellwood and Kelly, 2003). ^{14}C -dating of a 12 cm high stalked crinoid (*Gymnocrinus richeri*) indicates an age of 340 years (Richer de Forges *et al.*, 2004). Gorgonians from the family Isididae, can live over 300 years on New Caledonian seamounts and the age of larger colonies in New Zealand can be 500 years or more. The Isididae are characterized by their axis, which is composed of alternating nodes and internodes, the nodes consisting of horn and the internodes of massive crystalline calcareous substance (Noé and Dullo, 2006). Most species inhabit deep water. The axis of the gorgonians shows rings in cross-section (Fig. 7.6) and it is possible to use these sections to correlate the age and the variation of the rate Mg/Ca depending on water temperature. Surprisingly, in several samples from the Norfolk Ridge collected from depths of 500 m, a drop of temperature of about 2°C over 200 years was observed (Richer de Forges, 2001). In New Zealand, giant bubblegum gorgonian trees (*Paragorgia arborea*) were trawled on seamounts at the beginning of the orange roughy fisheries (see Chapter 19), and their age is estimated at 300–500 years (Tracey *et al.*, 2003). These slow-growing organisms are

very long lived, perhaps rivalling some of the well-known forest stands of ancient trees. More recently, preliminary studies using metal isotopes tracers have used the skeletons of deep-sea species as palaeo-environmental indicators (Ellwood and Kelly, 2003).

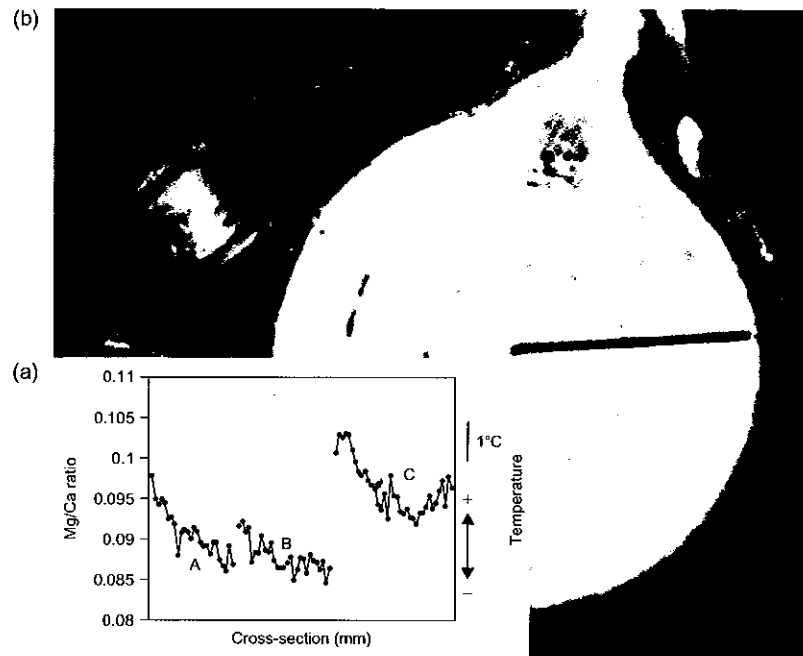


Fig. 7.6 Temperature measurement of three isidid gorgonians samples from Norfolk Ridge seamounts: (a) graphic with, on the left Mg/Ca (molar), on the right water temperature with the scale of 1°C on the graph and (b) cross-section of Isidid gorgonian showing the growth rings and the radial samples series. Source: After Richer de Forges (2001), modified by T. Corrège.

Environmental drivers of benthic diversity on seamounts

Data suggest that seamounts can be hotspots of biodiversity, but several of the reported key traits such as high endemism, archaism, slow growth rates and longevity may be an artefact of the greater sampling effort devoted to seamounts compared to other deep-sea habitats. However, the environmental factors that characterize seamounts may influence evolutionary and ecological processes leading to observed patterns of benthic diversity. Here we review these environmental factors and discuss how hypotheses about the origins seamount biodiversity may be tested.

Island effects

Seamounts differ from most other marine habitats by being spatially distinct and, arguably, isolated, topographic features. Most marine environments are relatively homogenous

and contiguous over large geographic scales, but seamounts generally occupy smaller and clearly defined areas. This geographic isolation evokes an analogy with terrestrial islands, and so seamounts have been viewed as isolated habitats with populations essentially stranded on them. The endemism and species richness in the terrestrial biota of oceanic islands are often explained by an acceleration of evolutionary processes due to physical barriers, fragmenting species into small isolated populations (Barton, 1998). However, the crucial difference is that seamounts are surrounded by water and most marine organisms can swim at one stage of their life cycle. It has, however, been suggested that the dispersion of benthic organisms during the pelagic stages of their life cycle is limited over seamounts by the hydrological phenomenon of Taylor caps (see Chapters 4 and 5; Roden, 1987). Indeed, it has been shown that in some cases the interaction between water circulation and topography promotes larval retention and aggregation (Boehlert and Mundy, 1993; Rogers, 1994; Mullineaux and Mills, 1997). Following this hypothesis, Mullineaux and Mills (1997) and Richer de Forges *et al.* (2000) suggested that this isolation could lead to a reduction in gene flow. Assessing the genetic structure of populations from different seamounts could test this hypothesis.

Resource availability and biomass

Seamounts often support sizeable fish stocks and are thus attractive fishing grounds. It is not always clear what mechanisms support the large fish stocks associated with seamounts, but some authors have proposed that seamounts are habitats of enhanced trophic subsidy (see Chapters 3 and 4). Several authors have suggested that the interaction between prominent topographic features and water masses increases turbulence and mixing, and enhances local biomass production by moving nutrients up into the euphotic zone (Fock *et al.*, 2002; Worm *et al.*, 2003; Genin, 2004). Enhanced biomass of filter feeders and other consumers should mirror any local concentration of seamount productivity. Indeed, our observations of benthic catches from the New Caledonian seamounts and nearby island slope indicate that the biomass of megabenthos, especially that of filter feeders, appears to be greater on seamounts. These observations of enhanced benthic biomass on seamounts have yet to be put to a quantitative test.

Consequences for life-history traits

Dispersal. If seamounts are isolated by physical barriers preventing larval dispersal, then gene flow should be reduced among populations, and swimming larvae should not confer an adaptive advantage. Thus, if the island hypothesis is correct, populations on seamounts should be genetically isolated and the proportion of species lacking larval dispersal should be greater than in other comparable environments.

Longevity. Some seamount species have particularly great longevity, and it is possible that environmental conditions and food on seamounts are relatively stable over long periods to permit such longevity. It has also been suggested that the longevity of benthic

organisms could be an adaptive solution to high variability of reproductive success (Flowers *et al.*, 2002). Neither of these hypotheses are particularly easy to test, as alternative explanations easily suggest themselves.

Gene flow and larval strategies

Genetic studies, of which there are few, permit evaluation of the isolation of seamount populations. Most studies concern fishes (Creasey and Rogers, 1999), many of which indicate isolation of populations at a local scale. For example, Aboim *et al.* (2005) demonstrated that populations of the benthopelagic fish *Helicolenus dactylopterus* were not isolated from one seamount to another, nor from the closest continental slope; genetic isolation among populations was found only at larger oceanic scales. The few genetic studies of benthic organisms from seamounts suggest the same pattern (e.g., Smith *et al.*, 2004). These results are comparable to the genetics of other isolated deep-sea habitats such as hydrothermal vents or cold seeps. Among vent organisms, bivalves from the genus *Bathymodiolus* disperse between very distant sites (Won *et al.*, 2003), and even between hydrothermal and cold-seep sites (Miyazaki *et al.*, 2004). Thus although these environments are markedly fragmented, species associated with these environments can be highly dispersive.

On seamounts, it seems that population fragmentation and restricted gene flow occur only for species with limited larval dispersal. Samadi *et al.* (2006) used benthic organisms from seamounts of the Norfolk Ridge to test whether physical and population fragmentation has encouraged high rates of speciation. If there is no larval retention, we would expect only species with poorly dispersive larvae to exhibit high genetic diversity. This was confirmed by two gastropod species that have contrasting larval dispersal strategies, inferred from the examination of the protoconch, and which allowed us to differentiate between the effects of their dispersal abilities and those of physical fragmentation resulting from hydrological phenomena. The non-planktotrophic species (*Nassaria problematica*) was highly structured, whereas the planktotrophic species *Sassia remensa*, was not. Similarly, five squat lobster species with dispersive larvae were genetically similar among populations on seamounts and the adjacent island slope. These results parallel deep-sea bamboo corals (Smith *et al.*, 2004) among which taxonomists had traditionally suggested a high rate of endemism on seamounts, and low gene flow among distant populations. A genetic survey confirmed that specific diversity is high, but showed that bamboo coral species are not endemic to seamounts and that distant populations are genetically interconnected.

Other studies on Atlantic seamounts revealed the same trends. In the North Atlantic, Gofas (2000) examining Fasciolaridae species, and Dijkstra and Gofas (2004) studying Pectinoidea species, found no seamount-to-seamount endemism, even between seamounts separated as much as 100 km. These results obtained for both planktotrophic and non-planktotrophic species, suggesting that seamounts are not highly isolated patches of habitat. Moreover, when comparing mollusc faunas from North Atlantic and Azores seamounts to the European mainland, planktotrophic development appears overrepresented (Gofas and Beu, 2002).

Overall, the few available studies suggest that, contrary to the island hypothesis, the hydrological phenomena associated with seamounts are not strong physical barriers and that populations of many organisms living on seamounts are genetically interconnected. However, this may not apply to all benthic seamount fauna, and should be regarded with caution because there are few data about the larval strategies of many deep-sea species. At Cobb Seamount (Parker and Tunnicliffe, 1994), a large portion of the 117 benthic species do not produce planktonic larva and only 6.8% have a long pelagic larval dispersal, observations supporting the island hypothesis.

Trophic architecture of seamount invertebrate benthos

Seamounts are commonly regarded as habitats where consumers proliferate in the otherwise food-poor environment of the deep ocean (Richer de Forges *et al.*, 2000). Amplified currents over seamounts enhance the growth of resident animals by augmenting the flux of suspended food (Genin, 2004). Hydrological processes that trap material over and around mounts can also locally enhance food resources (see Chapter 5; Rogers, 1994). One consequence of the increased supply of particles to these topographically abrupt habitats is that suspension feeders, such as corals and sponges, dominate the seamount megabenthos (Genin *et al.*, 1986; Wilson and Kaufmann, 1987).

This dominance of suspension feeders on seamounts (Genin *et al.*, 1986) suggests that benthic food webs of seamount may be simple. Because filter feeding is the chief trophic mode, most species would feed at low trophic levels and consume similar resources. The trophic architecture of the consumer guild is thus predicted to have low complexity, resulting in short food chains. However, recent trophic studies on New Caledonian seamounts have tested the hypothesis that food-chain length in seamount benthos is shorter than in other aquatic systems.

Food-chain length was determined with stable nitrogen isotope ratios ($\delta^{15}\text{N}$) measured in the tissues of a wide range of benthic invertebrate groups and some small fishes obtained as bycatch collected from several seamounts on the Norfolk Ridge. $\delta^{15}\text{N}$ is routinely used to determine the trophic position of consumers in food webs (Post, 2002) because $\delta^{15}\text{N}$ values are shifted by 3–4‰ towards more positive values during each trophic transfer (Minagawa and Wada, 1984). Thus, isotopic enrichment from prey to predator can be used to map the trophic level of consumers (Post *et al.*, 2000). Results show that food chains in seamount benthos are not short (Fig. 7.7), and the food web was not compressed to filter-feeding organisms that all feed at a similar trophic position (Fig. 7.7). In fact, the benthic food web on seamounts has a diverse trophic architecture with food-chain length broadly comparable to other aquatic systems, both shallow and deep (Table 7.4). Compared with other aquatic food webs, food-chain lengths in seamount benthos lie towards the upper end of reported values (Table 7.4). For non-seamount deep-sea food webs, measurements of maximum trophic position (MTP) range from 3.5 to 3.8 for the benthos of the Porcupine Abyssal Plain (Iken *et al.*, 2001), 4.6 in the Arctic Canada Basin (Iken *et al.*, 2005), to 4.5 in Astoria Canyon (Bosley *et al.*, 2004). Thus, food chains in the seamount invertebrate benthos – hypothesized to be shorter due to the dominance of suspension feeders – are in fact broadly similar in length to other deep-sea food webs. There

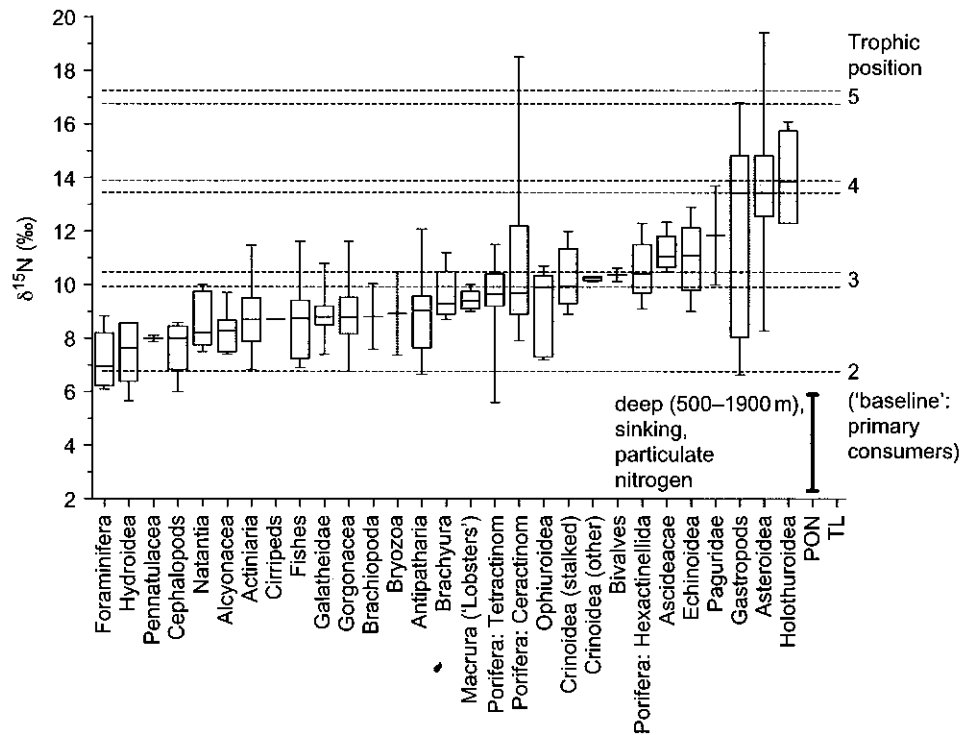


Fig. 7.7 Nitrogen isotope signature ($\delta^{15}\text{N}$) of the benthos on seamounts of the Norfolk Ridge. Isotope data from the seamounts are depicted as box and whisker plots (boxes: median plus 1st and 3rd quartile, whiskers: minimum and maximum values). Values for particulate organic nitrogen (PON) in sediment traps are from the literature (Altabet *et al.*, 1991, 1999; Altabet, 2001; Altabet and Francois, 2001; Lourey *et al.*, 2003). Calculation of trophic position is according to Post (2002): $\lambda + (\delta^{15}\text{N}_{\text{organism}} - \delta^{15}\text{N}_{\text{base of food web}}) / \Delta_n$, where λ is the trophic position of the organism used to estimate the 'baseline' of the food web (e.g., $\Delta_n = 2$ for primary consumers), and Δ_n is the enrichment per trophic transfer. We used a mean trophic fraction factor of 3.4 (Post, 2002), $\pm 95\%$ confidence limits of 0.26, depicted as dotted lines. We took primary consumers as the 'baseline' and this was calculated as the median of the first decile of all $\delta^{15}\text{N}$ measurements in the data set (it corresponds very well with an enrichment of 3–4 ppt from deep, particulate nitrogen to primary consumers).

Table 7.4 Comparison of food-chain length (measured as MTP sensu Post (2002) based on stable nitrogen isotopes) in aquatic food webs.

Source	Locality	Depth	MTP
Romanuk and Levings (2005)	Beaches, British Columbia	1 m	~4.2–4.5
Schlacher (unpublished)	Subtropical estuaries (Australia)	<10 m	3.8–4.0
Post <i>et al.</i> (2000)	Freshwater lakes ($n = 25$), N-America	<50 m	3.6–5.5
Jennings and Warr (2003)	North- and Irish Seas, English Channel	20–105 m	4.2–4.5
Le Loc'h and Hily (2005)	Bay of Biscay	95–120 m	3.6–4
Davenport and Bax (2002)	Continental Shelf, SE-Australia	20–250 m	3–3.8
Bosley <i>et al.</i> (2004)	Astoria Canyon, Oregon (USA)	89–549 m	3.9–4.5
This study	Seamounts Norfolk Ridge	200–900 m	4–5
Polunin <i>et al.</i> (2001)	Balearic Island Slope	200–1800 m	4.4
Iken <i>et al.</i> (2005)	Arctic, Canada Basin	625–3398 m	4.6
Iken <i>et al.</i> (2001)	Porcupine Abyssal Plain	4840 m	3.5–3.8

also appears to be little separation in terms of MTP between food-chain length on seamounts and shallow marine food webs (MTP: 3.8–4.5, Table 7.4) or even freshwater systems (MTP: 3.6–5.5; Post *et al.*, 2000). Our measurement of 4–5 trophic levels within the benthic consumer guild excludes larger predatory fish that may prey on the benthos. Thus, if benthopelagic predators were included in this type of analysis, the actual food-chain length of the seamount benthos may even be longer (Fig. 7.7).

Implications for conservation

Although the global status of seamount ecosystems remains underdocumented, several key biological traits of the benthos have important consequence to protect these systems. Seamount communities are highly vulnerable to the impacts of fishing because of (a) their limited habitat; (b) the extreme longevity of many species; (c) apparently limited recruitment between seamounts and (d) the highly localized distribution of many species. All of these factors combine to make seamounts highly vulnerable to human pressures. Bottom trawling is well known to be highly destructive activity on seamounts that sweeps away the benthic epifaunal community as 'bycatch' (see Chapter 19; Probert *et al.*, 1997; Koslow *et al.*, 2001; Batson, 2003). Although the negative impacts of bottom trawling on seamount biota are widely publicized, the practice continues throughout most of the world's oceans despite continuing efforts to highlight this issue (see Chapter 20; Willison *et al.*, 2001; Hall-Spencer *et al.*, 2002; Olu-LeRoy, 2004). Ironically, fish stocks may in part be dependent on the ecological condition of the seamount habitats, and rates of recovery are unknown for the seamount benthos following trawling impacts. Thus, temporary fishing closures may not be efficient in achieving long-term protection of seamounts, which rather requires the establishment and enforcement of permanent protection zones.

If the level of endemism on seamounts is as high as frequently reported or predicted, then the need for conservation of these habitats becomes critical. The highly localized distribution of many benthic seamount species increases the threat of possible extinctions, and as such may require that conservation measures of seamounts are designed and implemented on a local scale. Seamounts are also frequently referred to as highly productive and heterogeneous habitats, similar to rain forests or coral reefs. As such, they are predicted to accommodate large populations of many species and become target areas for protecting highly biodiverse areas (*sensu* Roberts, 2002). In theory, planning and implementation of conservation strategies for seamounts appear more readily achievable, at least from a spatial perspective, due to their geographically clearly defined nature.

Conclusions

Seamounts are unique habitats characterized by abrupt topographies, limited spatial extent, swift currents and hydrodynamic processes that can produce localized upwelling and

circulation cells. These environmental conditions are mirrored in a benthic biomass dominated by large suspension feeders that provide structural habitat for a great diversity of the smaller, mobile fauna. These diverse benthic assemblages contain species of limited geographic distribution (endemics) and species with ancient lineages or previously believed to have become extinct ('living fossils'). As a prominent seascape element that frequently rises well above the ocean floor, seamounts provide relatively shallow habitats for bathyal organisms amidst their abyssal surroundings. Invertebrates on seamounts tend to be slow-growing and long-lived, a life-history trait that makes them particularly vulnerable to human impacts such as bottom trawling. Although suspension feeders dominate the megabenthos, food webs are not simple and can rival other shallow and deep ecosystems in food-chain length and trophic architecture. While seamounts have frequently been likened to oceanic islands, their populations may not necessarily be genetically isolated if they produce larva capable of long-distance dispersal. Seamounts can also serve as 'natural laboratories' to test ecological theories like island biogeography in the marine realm.

Given the unique characteristics of seamounts and the diverse assemblages they support, it is surprising that the fauna remains poorly documented on a global scale. Whole assemblages are known only from a few seamounts worldwide, partly as a result of dwindling taxonomic resources. This lack of basic ecological knowledge currently constraints the development of more comprehensive models about the structure and function of the benthos, which would be conceptually applicable worldwide.

References

- Aboim, M.A., Menezes, G.M., Schlitt, T. and Rogers, A.D. (2005) Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. *Molecular Ecology*, 14, 1343–54.
- Altabet, M.A. (2001) Nitrogen isotopic evidence for micronutrient control of fractional NO_3^- utilization in the equatorial Pacific. *Limnology and Oceanography*, 46, 368–80.
- Altabet, M.A. and Francois, R. (2001) Nitrogen isotope biogeochemistry of the antarctic polar frontal zone at 170° W. *Deep-Sea Research, Part II: Tropical Studies Oceanography*, 48, 4247–73.
- Altabet, M.A., Deuser, W.E., Honjo, S. and Stienen, C. (1991) Seasonal and depth-related changes in the source of sinking particles in the North Atlantic. *Nature*, 354, 136–9.
- Altabet, M.A., Pilskalns, C., Thunell, R., Pride, C., Sigman, D., Chavez, F. and Francois, R. (1999) The nitrogen isotope biogeochemistry of sinking particles from the margin of the Eastern North Pacific. *Deep-Sea Research, Part I: Oceanographic Research Paper*, 46, 655–79.
- Amèziane-Cominardi, N., Bourseau, J.P. and Roux, M. (1987) Les crinoïdes pédonculés de Nouvelle-Calédonie (S.W. Pacifique): une faune ancestrale issue de la Mesogée mésozoïque. *Comptes rendus hebdomadaires de l'Académie des Sciences Paris*, 304(1), ser. 3, 15–18.
- Amèziane-Cominardi, N. (1991) Distribution bathymétrique des pentacrines du Pacifique occidental. Essai de modélisation et d'application aux faunes du Lias. *Documents Laboratoires de Géologie, Lyon*, 116, 253 pp, 5pl.

- Baba, K. (2005) Deep sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-Pacific, with a list of species. *Galathea Report*, 20, 1–317.
- Barton, N.H. (1998) Natural selection and random genetic drift as causes of evolution on islands. In: *Evolution on Islands* (ed. Grant, P.R.), pp. 102–23. Oxford University Press, Oxford.
- Batson, P. (2003) *Deep New Zealand. Blue Water, Black Abyss*, 240 p. Canterbury University press, Christchurch.
- Beaulieu, S.E. (2001) Life on glass houses: sponge stalk communities in the deep sea. *Marine Biology*, 138, 803–17.
- Boehlert, G.W. and Mundy, B.C. (1993) Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Sciences*, 53, 336–61.
- Bosley, K.L., Lavelle, J.W., Brodeur, R.D., Wakefield, W.W., Emmett, R.L., Baker, E.T. and Rehmke, K.M. (2004) Biological and physical processes in and around Astoria submarine Canyon, Oregon, USA. *Journal of Marine Systems*, 50, 21–37.
- Bouchet, P. and Metivier, B. (1982) Living Pleurotomariidae (Mollusca: Gastropoda) from the South Pacific. *New Zealand Journal of Zoology*, 9, 309–18.
- Bouchet, P., Lozouet, P., Maestrati, P. and Heros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75(4), 421–36.
- Bourseau, J.P., Améziane-Cominardi, N., Avocat, R., and Roux, M., (1991) Echinodermata: Les Crinoïdes pédonculés de Nouvelle-Calédonie. Résultats des Campagnes MUSORSTOM 8: 229–333.
- Cohen, B.L., Gawthrop, A. and Cavalier-Smith, T. (1998) Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. *Philosophical Transaction: Biological Sciences*, 353, 2039–69.
- Cohen, B.L., Améziane, N., Eleaume, M. and Richer de Forges, B. (2004) Crinoid phylogeny: a preliminary analysis (Echinodermata: crinoidea). *Marine Biology*, 144, 605–17.
- Creasey, S. and Rogers, A.D. (1999) Population genetics of bathyal and abyssal organisms. *Advances in Marine Biology*, 35, 3–151.
- Davenport, S.R. and Bax, N.J. (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries Aquatic Sciences*, 59, 514–30.
- Dijkstra, H., and Gofas, S., (2004). Penctinoidea Bivalvia: Propeamussiidae and Pectinidae from some northeastern Atlantic seamounts. *Sarsia: North Atlantic Marine Science*, 89: 33–78.
- Ellwood, M. and Kelly, M. (2003) Sponge 'tree rings'. *Marine biodiversity/Palaeoecology. Water and Atmosphere*, 11(2), 25–7.
- Flowers, J.M., Schroeter, S.C. and Burton, R.S. (2002) The recruitment sweepstakes has many winners: genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. *Evolution*, 56, 1445–53.
- Fock, H., Uiblein, F., Koester, F. and von Westernhagen, H. (2002) Biodiversity and species–environment relationships of the demersal fish assemblage at the Great Meteor Seamount (sub-tropical NE Atlantic), sampled by different trawls. *Marine Biology*, 141, 185–99.
- Genin, A. (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, 50, 3–20.
- Genin, A., Dayton, P.K., Lonsdale, P.F. and Spiess, F.N. (1986) Corals on seamounts provide evidence of current acceleration over deep sea topography. *Nature*, 322, 59–61.
- Gofas, S. (2000) Four species of the family Fasciolaridae (Gastropoda) from the North Atlantic seamounts. *Journal of Conchology*, 37, 7–16.
- Gofas, S. and Beu, A. (2002) Tonnoidean gastropods of the North Atlantic seamounts and the Azores. *American Malacology Bulletin*, 17, 91–108.

- Grigg, R.W., Malahoff, A., Chave, E.H. and Landahl, J. (1987) Seamount benthic ecology and potential environmental impact from manganese crust mining in Hawaii. In: *Seamounts, Islands and Atolls* (eds. Keating, B.H., Fryer, P., Batiza, R. and Boehlert, G.W.). *Geophysical Monographs*, 43, 379–90.
- Hall-Spencer, J., Allain, V. and Fossa, J.H. (2002) Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society of London B*, 269, 507–11.
- Heinz, P., Ruepp, D. and Hemleben, C. (2004) Benthic foraminifera assemblages at Great Meteor Seamount. *Marine Biology*, 144, 985–98.
- Hess, H., Ausich, W.I., Brett, C.E. and Simms, M.J. (1999) *Fossil Crinoids*, 275 p. Cambridge university press, Cambridge.
- Iken, K., Bluhm, B.A. and Gradinger, R. (2005) Food web structure in the high Arctic Canada Basin: evidence from delta C-13 and delta N-15 analysis. *Polar Biology*, 28, 238–49.
- Iken, K., Brey, T., Wand, U., Voigt, J. and Junghans, P. (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress in Oceanography*, 50, 383–405.
- Jennings, S. and Warr, K.J. (2003) Environmental correlates of large-scale spatial variation in the delta N-15 of marine animals. *Marine Biology*, 142, 1131–40.
- Johannesson, K. (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology*, 99, 507–13.
- Kelly, M. (2000) Description of a new lithistid sponge from northeastern New-Zealand, and consideration of the phylogenetic affinities of families Corallistidae and Neopeltidae. *Zoosystema*, 22(2), 2–18.
- Koslow, J.A. and Gowlett-Holmes, K. (1998) The seamount fauna off southern Tasmania: benthic communities, their conservation and impacts of trawling. *Report to the Environmental Australia Fisheries Commission 95/058*.
- Koslow, J.A., Gowlett-Holmes, K., Lowry, J., O'Hara, T., Poore, G. and Williams, A. (2001) The seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology Progress Series*, 213, 111–25.
- Kuznetsov, A.P. and Mironov A.N. (eds.) (1981) *Benthos of the Submarine Mountains Marcus-Necker and Adjacent Pacific Regions*. Academy of Sciences of the USSR P.P. Shirshov Institute of Oceanology, Moscow.
- Laurin, B. (1992) Decouverte d'un squelette de soutien du lophophore de type 'crura' chez un brachiopode inarticulé: description de *Neoancistrocrania norfolki* gen. sp. nov. (Cranidae). *Comptes rendus hebdomadaires de l'Académie des Sciences, Paris*, 314, ser. 3, 343–50.
- Laurin, B. (1997) Brachiopoda: brachiopods récoltés dans les eaux de la Nouvelle-Calédonie et des îles Loyauté, Matthew et Chesterfield. In: Résultats des campagnes MUSORSTOM (ed. Crosnier, A.), Vol. 18. *Mémoires du Muséum national d'Histoire naturelle*, 176, 413–73.
- Lawton, J.H. and May, R.M.C. (1995) *Extinction Rates*. Oxford University Press, Oxford.
- Le Loc'h, F. and Hily, C. (2005) Stable carbon and nitrogen isotope analysis of *Nephrops norvegicus Merluccius merluccius* fishing grounds in the Bay of Biscay (Northeast Atlantic). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 123–32.
- Lévi, C. (1991) Lithistid sponges from the Norfolk Rise. Recent and Mesozoic Genera. In: *Fossil and Recent Sponges* (eds. Reitner, J. and Keupp, H.), pp. 72–82. Springer-Verlag, Berlin/Heidelberg.
- Lourey, M.J., Trull, T.W. and Sigman, D.M. (2003) Sensitivity of delta N-15 of nitrate, surface suspended and deep sinking particulate nitrogen to seasonal nitrate depletion in the Southern Ocean – Art. No. 1081. *Global Biogeochemical Cycles*, 17, 1081.

- Macpherson, E. and Machordom, A. (2005) Description of three sibling new species of the genus *Munida* Leach, 1820 (Decapoda, Galatheidae) from New Caledonia using morphological and molecular data. *Journal of Natural History*, 39, 819–34.
- Minagawa, M. and Wada, E. (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochemica et Cosmochemica Acta*, 48, 1135–40.
- Miyazaki, J.I., Shintaku, M., Kyuno, A., Fujiwara, Y., Hashimoto, J. and Iwasaki, H. (2004) Phylogenetic relationships of deep-sea mussels of the genus *Bathymodiolus* (Bivalvia: Mytilidae). *Marine Biology*, 144, 527–35.
- Mullineaux, L.S. and Mills, S.W.A. (1997) A test of the larval retention hypothesis in seamount-generated flows. *Deep-Sea Research Part I: Oceanographic Research Papers*, 44, 745–70.
- Noé, S.U. and Dullo, W.C. (2006) Skeletal morphogenesis and growth mode of modern and fossil deep-water isidid gorgonians (Octocorallia) in the West Pacific (New Zealand and Sea of Okhotsk). *Coral Reefs*, DOI 10.1007/s00338-006-0095-8.
- Olu-Le Roy P.K. (2004). Deep water corals: biodiversity to be evaluated and preserved. *Vertigo* 5: 1–10.
- Parin N.V., Mironov, A.N. and Nesis, K.N. (1997) Biology of the Nazca and Sala y Gómez submarine ridges, an outpost of the Indo-West Pacific fauna in the eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. *Advances in Marine Biology*, 32: 145–242.
- Parker, T. and Tunnicliffe, V. (1994) Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *Biological Bulletin*, 187, 336–45.
- Polunin, N.V.C., Morales-Nin, B., Pawsey, W.E., Cartes, J.E., Pinnegar, J.K. and Moranta, J. (2001) Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series*, 220, 13–23.
- Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703–18.
- Post, D.M., Pace, M.L. and Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047–9.
- Probert, P.K., McKnight, D.G. and Grove, S.L. (1997) Case studies and reviews. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 7, 27–40.
- Richer de Forges, B. (2001) Les faunes bathyales de l'Ouest Pacifique: diversité et endémisme. Mémoire d'Habilitation à diriger des recherches. Université Pierre et Marie Curie, Paris, Vol. 1, 83 pp.
- Richer de Forges B. (2006) Découverte en mer de Corail d'une deuxième espèce de glypheide (Crustacea, Decapoda, Glypheoidea). *Zoosystema*, 28(1), 17–29.
- Richer de Forges, B., Koslow, J.A. and Poore, G.C. (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature*, 405, 944–7.
- Richer De Forges, B., Grandperrin, R. and Laboute, P. (1987) La Campagne CHALCAL II sur les guyots de la ride de Norfolk (N.O. CORIOLIS, 26 Octobre-Ler Novembre 1986). Rapports Scientifiques et techniques, sciences de la mer, Rep. 42, Institut Français de recherche scientifiques pour le développement en coopération.
- Richer de Forges, B., Corrège, T. and Paterné, M. (2004) Estimation de la longévité chez les organismes de profondeur. *Assises de la Recherche française dans le Pacifique, 23–27 août 2004*, Nouméa (poster).

- Richer de Forges, B., Hoffschir, C., Chauvin, C. and Berthault, C. (2005) Inventaire des espèces de profondeur de Nouvelle-Calédonie/Census of deep-sea fauna in New Caledonia. *Rapport Scientifique et Technique* 116, volume spécial. IRD Nouméa: 113 p.
- Richer de Forges, M. (2001) Endémisme du benthos des monts sous-marins de la ride de Norfolk (Pacifique sud-ouest): éponges et mollusques gastéropodes. *Rapport de Maîtrise de Biologie des populations et écologie, Université Pierre et Marie Curie*, 39 p.
- Richer de Forges, S. (2001) Analyse des paléotempératures mesurées sur des squelettes de gorgones Isididae de profondeur. *Rapport de stage de DEUG: IRD/Nouméa* (Maître de stage Thierry Corrège), 11 p.
- Roberts, C.M. (2002) Deep impact: the rising toll of fishing in the deep sea. *TREE*, 17, 242–5.
- Roden, G.I. (1987) Effects of seamounts and seamount chains on oceanic circulation and thermocline structure. In: *Seamounts, Islands and Atolls* (eds. Keating, B.H. et al.), pp. 335–54. *Geophysical Monographs*, ser 43. AGU, Washington, DC.
- Rogers, A.D. (1994) The biology of seamounts. *Advances in Marine Biology*, 30, 305–50.
- Romanuk, T.N. and Levings, C.D. (2005) Stable isotope analysis of trophic position and terrestrial vs. marine carbon sources for juvenile Pacific salmonids in nearshore marine habitats. *Fisheries Management and Ecology*, 12, 113–21.
- Samadi, S., Bottan, L., Macpherson, E., Richer de Forges, B. and Boisselier, M.C. (2006) Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. *Marine Biology*, DOI 10.1007/s00227-006-0306-4.
- Schlacher-Hoenlinger, M.A., Pisera, A. and Hooper, J.N.A. (2005) Deep-sea lithistid assemblages from the Norfolk ridge (New Caledonia), with description of seven new species and a new genus (Porifera, Demospongiae). *Zoosystema*, 27(4): p. 649–98.
- Smith, D.K. and Jordan, T.H. (1988) Seamount statistics in the Pacific Ocean. *Journal of Geophysical Research*, 93, 2899–919.
- Smith, P.J., McVeagh, S.M., Mingoia, J.T. and France, S.C. (2004) Mitochondrial DNA sequence variation in deep-sea bamboo coral (Keratoisidinae) species in the southwest and northwest Pacific Ocean. *Marine Biology*, 144, 253–61.
- Stocks, K. (2005) Seamounts Online: an online information system for seamount biology. Version 2005-1. World Wide Web electronic publication. <http://seamount.sdsc.edu>.
- Tracey, D., Neil, H., Gordon, D. and O'Shea, S. (2003) Chronicles of the deep: ageing deep-sea corals in New Zealand waters. *Marine Biodiversity. Water and Atmosphere*, 11(2), 22–4.
- Vacelet, J., Cuif, J.P., Gautret, P., Massot, M., Richer de Forges, B. and Zibrowius, H.A. (1992) Colonial sphinctozoan sponge related to triassic reef builders surviving in deep water off New Caledonia. *Comptes rendus hebdomadaires de l'Académie des Sciences, Paris*, 314, 379–85.
- Van de Beuque, S. (1999) Evolution géologique du domaine peri-calédonien (Sud ouest Pacifique). *Thèse de doctorat de l'Université de Bretagne occidentale, 19 mars 1999*, 270 p.
- Veevers, J.J. (2000) *Billion-Year Earth History of Australia and Neighbours in Gondwanaland*, 388 p. GEMOC Press, Sydney.
- Veevers, J.J. (2001) *Atlas of Billion-Year Earth History of Australia and Neighbours in Gondwanaland*, 76 p. GEMOC Press, Sydney.
- Verlaan, P.A. (1992) Benthic recruitment and manganese crust formation on seamounts. *Marine Biology*, 113(1): p. 171–4.
- Willison, J.H., Hall, J., Gass, S.E., Kenchington, E.L.R., Butler, M. and Doherty, P. (2001) *Proceedings of the First International Symposium on Deep-Sea Corals. Ecology Action Centre. Nova Scotia Museum, Halifax*, 231 p.

- Wilson, R.R. and Kaufmann, R.S. (1987) Seamount biota and biogeography. In: *Seamounts, Islands and Atolls* (eds. Keating, B.H., Fryer, P., Batiza, R. and Boehlert, G.W.). *Geophysical Monographs*, 43, 355–77.
- Won Y., Hallan, S.J., O'Mullan, G.D. and Vrijenhoek, R.C. (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiolus*) from eastern Pacific hydrothermal vents. *Molecular Ecology*, 12, 3185–90.
- Worm, B., Lotze, H.K. and Myers, R.A. (2003) Predators diversity hotspots in the blue ocean. *Proceedings of Natural Academy of Sciences USA*, 100, 9884–8.