

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Pante, E., L. Corbari, J. Thubaut, T.-Y. Chan, R. Mana, M.-C. Boisselier, P. Bouchet, and S. Samadi. 2012. Exploration of the deep-sea fauna of Papua New Guinea. *Oceanography* 25(3):214–225, <http://dx.doi.org/10.5670/oceanog.2012.65>.

DOI

<http://dx.doi.org/10.5670/oceanog.2012.65>

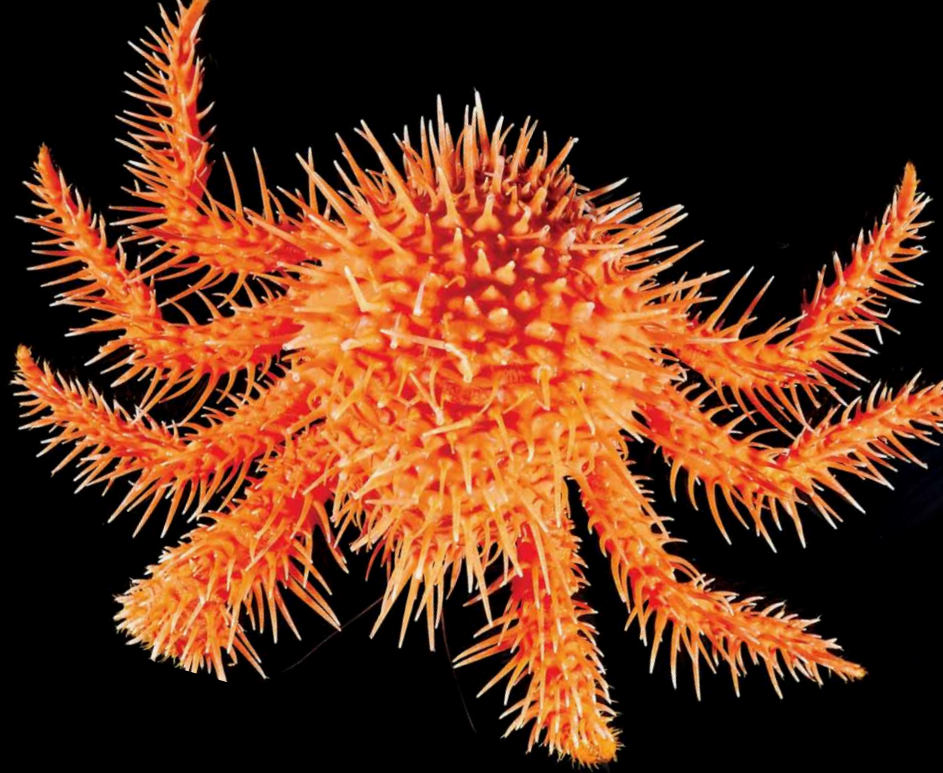
COPYRIGHT

This article has been published in *Oceanography*, Volume 25, Number 3, a quarterly journal of The Oceanography Society. Copyright 2012 by The Oceanography Society. All rights reserved.

USAGE

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: info@tos.org or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.

LEFT | A freshly collected specimen of the spider crab *Oxypleurodon christiani*, newly described from the BioPapua collections (Richer de Forges and Corbari, 2012). TOP AND BOTTOM | Specimens of king crabs preliminarily attributed to the genus *Paralomis*.



Exploration of the Deep-Sea Fauna of Papua New Guinea

BY ERIC PANTE,
LAURE CORBARI,
JUSTINE THUBAUT,
TIN-YAM CHAN,
RALPH MANA,
MARIE-CATHERINE BOISSELIER,
PHILIPPE BOUCHET,
AND SARAH SAMADI



ABSTRACT. Little is known of New Guinea's deep benthic communities. In fall 2010, the Muséum national d'Histoire naturelle, Institut de Recherche pour le Développement, and University of Papua New Guinea spearheaded an international three-leg cruise, BioPapua, aimed at exploring the deep waters of eastern Papua New Guinea and its satellite islands. Special attention was given to faunal assemblages associated with sunken wood and decomposing vegetation as well as seamount summits and slopes. In this article, we review the information available on the deep ecosystems of Papua New Guinea and summarize preliminary results of the BioPapua cruise.

NEW GUINEA AND OUR UNDERSTANDING OF BIODIVERSITY

The island of New Guinea has a special place in the heart of biologists. Biodiversity studies in New Guinea and its satellite islands have helped shape some of the pillars of evolutionary biology and ecological theory. In the late 1850s, New Guinea was the eastern-most of Alfred Wallace's destinations during his exploration of the Malay Archipelago, and his comparative observations nurtured his theories on island biogeography and the mechanisms promoting evolution (Wallace, 1869, 1876). In the 1920s, ornithologist Ernst Mayr accumulated data on New Guinea birds that would later appear in his *Systematics and the Origin of Species*, a landmark in the development of the modern synthesis (Mayr, 1942). Similarly, data from New Guinean ant diversity found their place in MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson, 1967). Jared Diamond's observations of the bird fauna of New Guinea and its satellite islands nourished his work on the structure of ecological communities and fed the "Single Large Or Several Small [SLOSS]" debate on the application of the principles of biogeography in reserve design and conservation biology (Diamond, 1972, 1973,

1975). More recently, research conducted in New Guinea by Vojtech Novotný and collaborators on plant-insect host specificity has bearing on global biodiversity numbers (e.g., Novotný et al., 2002; Hamilton et al., 2010). And then, of course, there is Tim Flannery's immensely popular *Throwim Way Leg*, a travelogue that perpetuates our perception of New Guinea as a frontier of biodiversity exploration (Flannery, 1998). The faunal diversity of the island's terrestrial, shallow marine, and coral environments is well known; the island is nestled in the middle of the Coral Triangle, a zone delineated by Taiwan, Bali, and the Solomon Islands that is home to about three quarters of the world's coral species (Veron et al., 2009).

In contrast, there is a surprising lack of information on the deep-sea ecosystems surrounding New Guinea and its satellite islands. Symptomatically, the *Challenger* expedition sailed almost directly from Torres Strait to Hong Kong and the Philippines; though it visited the Admiralty Islands in the Bismarck Sea from March 4–10, 1875, only a single deepwater haul was made in 150 fathoms; likewise, the Dutch *Siboga* expedition (1899–1900) did not sample east of Halmahera. In fact, of the "historical" exploring expeditions, only the Danish *Galathea* (1950–1952) and the Russian

Vityaz expeditions collected biological benthic samples in the region, namely the hadal part of the New Britain Trench in the Solomon Sea (Belyaev, 1972).

In fall 2010, the Muséum national d'Histoire naturelle (MNHN) and the Institut de Recherche pour le Développement (IRD; France), in collaboration with the University of Papua New Guinea (UPNG), put together a team of international scientists to explore and describe the deep benthic fauna of the Bismarck and Solomon Seas. The research cruise BioPapua mobilized 11 scientists from six countries, who occupied 156 stations within 2–9°S and 144–155°E (Figure 1). In this article, we review the available information on the deep-sea environments of Papua New Guinea (PNG), and describe the efforts deployed for the BioPapua cruise.

THE DEEP-SEA ENVIRONMENTS OF PAPUA NEW GUINEA

PNG is situated in one of the most geologically active regions in the world, where all possible types of plate boundaries can be observed (Tregoning et al., 2000). Most of the tectonic energy results from the collision of the Indo-Australian and Pacific Plates, which entrap the Bismarck, Solomon, and Woodlark Plates (e.g., Tregoning et al., 2000; Hall, 2002). To the north, the Manus Basin

The authors wish to dedicate this feature to Christian Késiano Fitialeata, who tragically passed away during the first leg of BioPapua. Christian had been a crew member on R/V Alis for many years, and was instrumental in the success of many cruises of the Tropical Deep-Sea Benthos program. He was a great companion at sea and on land, and is sorely missed.

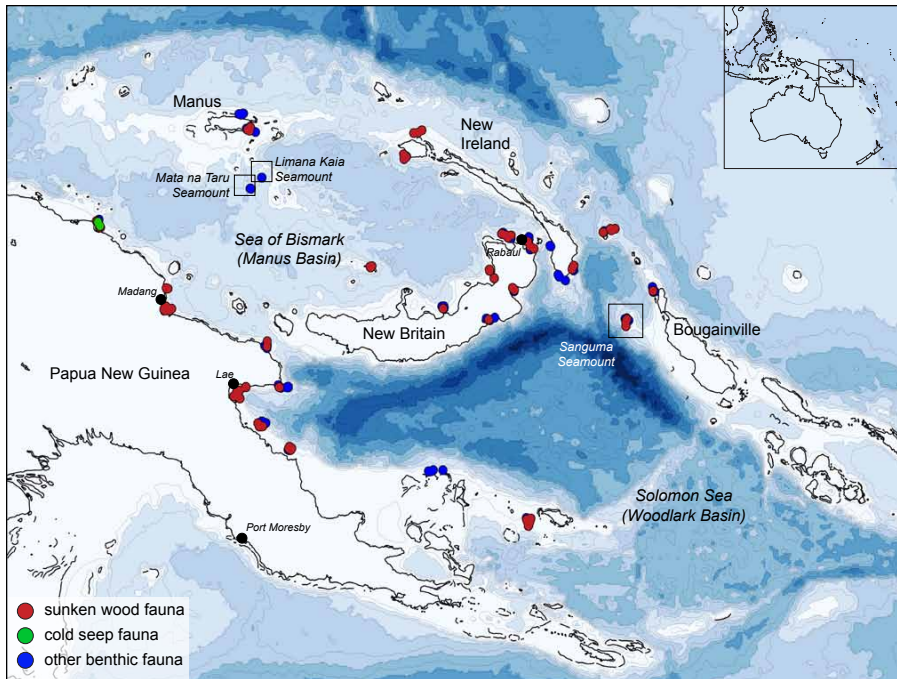


Figure 1. Map of Papua New Guinea and its satellite islands. Dots, color-coded based on faunal type, represent sampling stations. The inset provides a regional map. A marine geological map of PNG can be found in Tregoning et al. (2000).

recently formed (< 4 million years ago) in the Bismarck Sea. This sedimentary basin is characterized by several active accretion zones (the Manus Spreading Center, the South Eastern Rift, and the Western Rift zones) and is rapidly spreading. To the south, the young Woodlark Basin (formed < 2.5 million years ago) produces new oceanic crust, while the Solomon Plate subducts beneath the Bismarck Plate, forming the New Britain chain.

Most of the biological deep-sea scientific exploration done to date in the PNG region stemmed from geological research. PNG's strong tectonic activity is particularly conducive to hydrothermal venting, which was first revealed in the mid- to late 1980s (Both et al., 1986; Tufar 1990; Lisitsyn et al., 1993). A series of international research efforts followed, with cruises involving American, Canadian, Australian, Japanese, Russian,

German, Austrian, and French teams (Auzende et al., 2000, and references therein). These efforts mostly focused on the Pacmanus and Vienna Woods vent fields in the Bismarck Sea, and on Franklin Seamount in the Solomon Sea.

The geological complexity and the rapidity of change observed in the area are of particular biogeographic interest, both in terms of biological colonization and diversity of habitat (e.g., hydrothermal vent fields, river sedimentary cones, seamounts, slopes and canyons, sedimentary plains). Significant efforts have been made to describe the endemic hydrothermal-vent fauna (e.g., Desbruyères et al., 2006, and references therein), but the general deep benthic fauna have yet to be described. For example, the Ocean Biogeographic Information System (OBIS) database contains information on 34 species of deepwater crustaceans, 30 of which are

vent endemic, a very meager inventory for an exclusive economic zone (EEZ) totaling over 2 million km² of benthic surface below 100 m depth (Vanden Berghe, 2007; Edward Vanden Berghe, OBIS, *pers. comm.*, 2011). The Bismarck and Solomon Seas host many underwater features such as seamounts, of which only a very few (e.g., Franklin and Edison Seamounts) have been sampled, mapped, or even visited. Allain et al. (2008) recently reviewed the seamounts of the southwestern Pacific by screening and cross checking 20 existing data sets, and listed 91 underwater features for the EEZ of PNG. No information is available for 69 of those features. The 22 other features were further classified into seamounts (11), drowned atolls and banks (7 and 1), ridges (2), and a plateau. This lack of information on PNG seamounts is reflected by the fact that no seamount site is available on the Seamount Online or Seamount Catalogue databases, not even the few that have been sampled.

NEW GUINEAN DEEP BENTHIC FAUNA IN A REGIONAL BIOGEOGRAPHIC CONTEXT

The current body of knowledge on New Guinean deep-sea benthic fauna comes almost exclusively from the study of highly specialized hydrothermal vent animals, the distribution of which strictly depends on the location of vent fields. Hydrothermal vent animals might therefore not be good models to represent the biology of deep New Guinean fauna. Data on other benthic groups, however, are sorely lacking, and do not allow us to understand patterns of faunal connectivity across the deep waters of the western Pacific Ocean at this time. This section summarizes

current knowledge on the biogeography of deep-sea benthic organisms in the western Pacific Ocean.

Studies of the global biogeography of hydrothermal vent fauna place New Guinean assemblages within a Southwestern Pacific Province. In the analysis of Bachraty et al. (2009), the Mariana back-arc basin, Loihi Seamount offshore Hawaii, seamounts of the Kermadec Arc in New Zealand, and the Central Indian Ridge delimit this region. Previous studies offer different boundaries for this province (e.g., Van Dover et al., 2002; Tyler and Young, 2003) but show faunal affinities between New Guinean vents and the Mariana, North Fiji, and Lau back-arc basins. These affinities, however, are relatively weak, as most vents are characterized by high endemism at the species level. In a multivariate community analysis, Desbruyères et al. (2006) found that the highest similarity level between vents of the Manus basin and other Southwest Pacific locations was 24% at the species level and 46% at the genus level, and linked the New Guinean vents to the communities of the North Fiji and Lau back-arc basins. In fact, Vrijenhoek (2010) and Van Dover (2011) recently proposed a biogeographic model in which New Guinean vents constitute the northwestern end of the range of a distinct Southwestern Pacific Province. The New Guinean back-arc basins are particularly isolated within the mosaic of western Pacific spreading centers, as about 1,500 km separate the Woodlark Basin from North Fiji and Manus from the Mariana Basin (Hessler and Lonsdale, 1991).

The geographic isolation of PNG hydrothermal-vent organisms may have

strongly affected their evolutionary history and current distribution. This fauna may therefore not be representative of the overall biogeography of deep-sea benthic fauna from this area. Unfortunately, data from other deep-sea organisms are very scarce. The known biogeography of the deep-sea coral genus *Chrysogorgia* well exemplifies the lack of information on nonvent, deep benthic fauna (Figure 2; Pante et al., 2012). *Chrysogorgia* shows sampling gaps around PNG indicative of our state of knowledge on the New Guinean deep-sea fauna. Out of 65 species (and variations), 21 were originally described from locations in or on the immediate periphery of the Coral Triangle. Although five species from the Malay Archipelago were also observed in the Northeast Pacific (Hawaiian Archipelago), only two species were found to occur both east and west of the island of New Guinea. Although these results might simply be a sampling artifact or the result of incomplete taxonomic knowledge, they might also reflect actual biogeographic patterns.

Other invertebrate models suggest a dichotomy between northern and southern biogeographic provinces. In a large-scale analysis of squat lobster biogeographic patterns, Macpherson et al. (2010) established that the fauna of the Coral Sea (New Caledonia, Vanuatu, and the Solomon Islands) was significantly different from the species assemblages found in eastern Australia, Indonesia (Banda and Celebes Seas), and the Philippines. No data were available for PNG. Similar biogeographic studies focusing on deep-sea bathymodioline mussels support the same overall geographic separations, with mussel assemblages being very similar among New Caledonia, Vanuatu, and the Solomon Islands, and different from northern locations such as the Philippines (Lorion et al., 2010; Lorion and Samadi, 2010). Again, no data were available for PNG. Puillandre et al. (2010), questioning how modes of larval dispersal relate to geographical fragmentation in the gastropod *Bathytoma* in the western Pacific, also underlined the sore lack of

Eric Pante was a PhD candidate at the University of Louisiana at Lafayette (USA) during the BioPapua cruise, and is now a postdoctoral researcher at the Laboratoire Littoral, Environnement et Sociétés (LIENSs), Université de La Rochelle, La Rochelle, France.

Laure Corbari is Assistant Professor, Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France. **Justine Thubaut** is PhD Candidate, Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France.

Tin-Yam Chan is Professor, Institute of Marine Biology and Center of Excellence for Marine Bioenvironment and Biotechnology, National Taiwan University, Taiwan. **Ralph Mana** is Professor, School of Natural and Physical Sciences, University of Papua New Guinea, Port Moresby, Papua New Guinea. **Marie-Catherine Boisselier** is a researcher at the Centre National de la Recherche Scientifique, working at the Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France. **Philippe Bouchet** is Professor, Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France. **Sarah Samadi** (sarah@mnhn.fr) is a researcher at the Institut de Recherche pour le Développement, working at the Muséum national d'Histoire naturelle, Département Systématique et Evolution, Paris, France.

specimens from New Guinea.

It is clear from hydrothermal vent community data available today, as well as from the biogeographic patterns of corals, galatheid crabs, and bathymodioline mussels, that the deep waters of PNG are located at the confluence of different biogeographic regions. The foundations of our exploration of PNG deep benthic ecosystems are therefore both discovery- and hypothesis-driven, as we aim to document the deepwater benthic organisms present in nonhydrothermal ecosystems and to understand their historical and contemporary biogeography in the context of the tropical Western Pacific. Are organisms from this region more closely related to southern, northern, or western species pools? What are

the historical and contemporary mechanisms leading to the faunal discontinuities within the region?

BIOPAPUA AND THE TROPICAL DEEP-SEA BENTHOS PROGRAM

BioPapua is part of a long-term research endeavor called the Tropical Deep-Sea Benthos (TDSB) program. Started in the 1980s by the IRD (formerly Office de la Recherche Scientifique et Technique Outre-Mer [ORSTOM]) and the MNHN, its goal is to explore the deep benthic ecosystems of the tropical Indo-West Pacific, with special emphasis on macroinvertebrates. Since the late 1970s, more than 60 TDSB cruises have been conducted from Taiwan to the Marquesas Islands, and sampling was

conducted at over 5,000 stations between 100 and 1,500 m depth. Through taxonomic networking with an international team of more than 200 scientists, over 2,000 new species have been described based on material from the TDSB program (Bouchet et al., 2008).

TDSB cruises, because of their robustness and relative technical simplicity, often represent the first-ever exploration of the deep-sea benthos in remote areas such as Tonga, the Solomon Islands, or Vanuatu. BioPapua, as most TDSB cruises, relied on the New Caledonia-based R/V *Alis*, a 28 m long ship with high maneuverability. The combined use of a beam trawl and a dredge maximizes the types of substrates and faunal diversity that can be collected (Figure 3).

BIOPAPUA RESEARCH THEMES AND PRELIMINARY RESULTS

The first purpose of BioPapua, as for previous TDSB cruises, was to explore remote and uncharted territory and describe its deep benthic fauna. Beyond this effort of discovery, BioPapua was designed to sample specimens from targeted habitats and address specific questions on the evolution of deep-water invertebrates. We outline research themes and preliminary results below.

Sunken Wood and the Evolution of Chemosynthetic Organisms

Since their discovery in 1977 on the Galápagos Spreading Center (Lonsdale, 1977), hydrothermal vents have been the focus of tremendous research interest. Although significant efforts were put forth to characterize this environment and elucidate the mechanisms involved in its functioning and maintenance, much less is

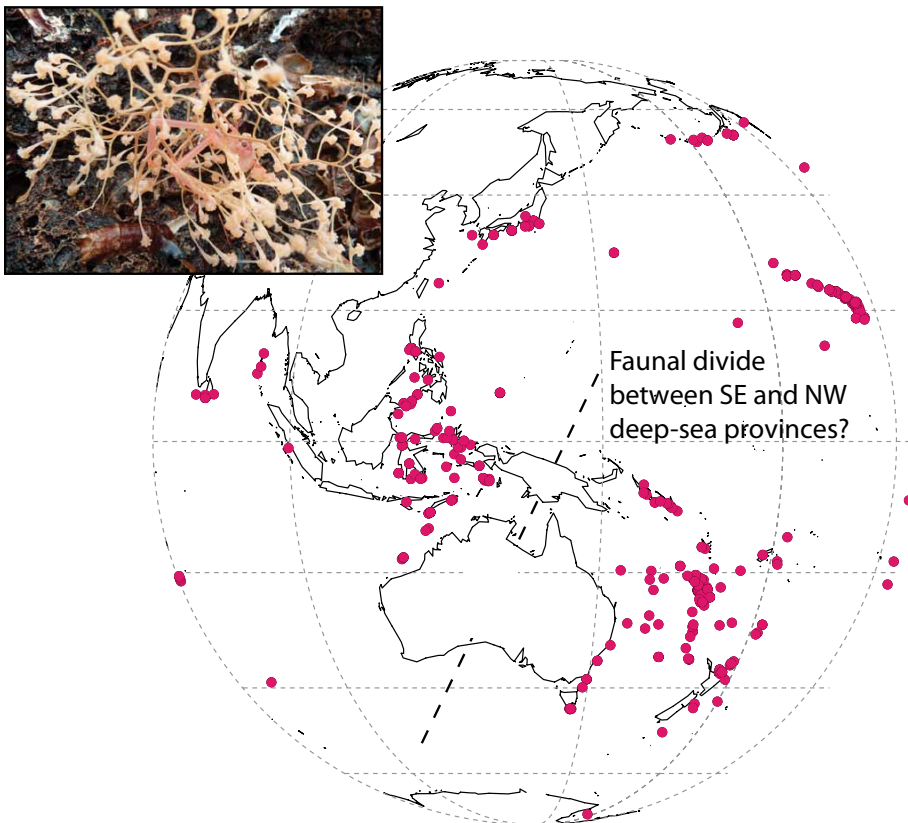


Figure 2. Geographic distribution of 634 records of the octocoral genus *Chrysogorgia*. Inset: one of the 56 colonies of *Chrysogorgia* sampled during BioPapua, with associated squat lobster (data from Watling et al., 2011).

known about the evolutionary origins of its fauna. Phylogenetic studies of the deep-sea mussels of the subfamily Bathymodiolinae show that species from vents, seeps, and deep-sea organic falls (vegetation and whale carcasses) form monophyletic clades, suggesting that these deep-sea bivalves may have used organic falls as a transitional habitat from shallow habitats to deep vents and seeps (Distel et al., 2000). Recent results suggest that the evolutionary history of deep-sea mussels associated with organic falls is completely tangled with that of vent and seep mussels, with scenarios probably more complex than the “wooden steps” hypothesis (Lorion et al., 2010). Moreover, geography, rather than habitat specificity or chemosymbiotic requirements, seems to significantly structure diversification patterns in sunken wood-associated mytilids (Lorion et al., 2009, 2010).

There are still large gaps in our understanding of the series of evolutionary events that lead to the diversification of vent, seep, and organic fall fauna. First, sampling plays a crucial role in comparative phylogenetic inference, and most studies to date are biased toward a more robust sampling of vents and seeps. Incomplete sampling can lead to phylogenies that do not accurately reflect evolutionary history. There is therefore a need to thoroughly characterize both vent/seep and organic fall biodiversity. One objective of BioPapua was to provide new material that may promote understanding of the evolutionary origins of the crustaceans and mollusks inhabiting deep-sea chemosynthetic environments. To fill the identified sampling gaps, the main objectives are (1) to describe the

diversity (morphological, genetic, and ecological) associated with organic falls, (2) to determine how organisms rely on organic remains, and (3) to investigate the historical and ecological factors that may have influenced the diversification of this fauna.

Among the 156 stations sampled during BioPapua, 84 contained sunken vegetation. A wide array of bays and submarine canyons was sampled, from the mouth of the Sepik River to Mambare Bay on the eastern coast of the island of New Guinea, and on the eastern and western coasts of New Britain. Trawling revealed a wealth of decomposing wild and cultivated plants (tree trunks, branches and leaves, sugar cane, coco, and nypa nuts). Decaying vegetation was found accumulating at the bottom of submarine canyons. As expected, these substrates were host to

a unique fauna, composed of mollusks (wood-boring bivalves and mytilids, chitons, gastropods; see Warén, 2011), crustaceans (isopods, amphipods, barnacles, and decapods), echinoderms (sea urchins, sea stars, and ophiuroids), polychaetes (19 families identified so far), and sipunculids (see Figure B1 in Box 1), a composition that was consistent with previous findings from other locations in the Southwest Pacific (Samadi et al., 2010). For example, the crustaceans collected on plant remains belong to a few genera repeatedly found on such material throughout the Indo-Pacific (for decapods: the galatheids *Munida* and *Munidopsis*, the hermit crabs *Xylopagurus* and *Pylocheles*, and the thalassinids *Callianassa*; Samadi et al., 2010). Most of the taxa, however, probably belong to new species. Author Thubaut and colleagues included nine



Figure 3. Sampling strategy employed during BioPapua and other Tropical Deep-Sea Benthos cruises. (a) Beam trawl. (b) Warén dredge. (c–d) Raw samples that illustrate the abundance of fauna collected and the diversity of substrates.

BOX 1. VEGETATION-ASSOCIATED FAUNA

The *Challenger* expedition (1872–1876) casually documented the presence of animals on plant remains at the deep seafloor, but the importance of plant material in the deep sea was not underscored until Wolff (1979). Until recently, plant-associated organisms were mainly looked at as zoological and/or ecological curiosities and thus (apart from taxonomic consideration) only anecdotally studied. During previous TDSB cruises in the Solomon Islands, it became clear that the slopes of oceanic islands within the region accumulate large amounts of decomposing vegetation. Organic debris was associated with a rich and original fauna (Samadi et al., 2007a; Warén, 2011), and its discovery catalyzed new research interests for the TDSB team (Samadi et al., 2010). Subsequent cruises in the Solomon Islands and Vanuatu specifically targeted sunken vegetation to further characterize this fauna. PNG and its satellite islands appear to be a very promising location for such studies. Their lush coastal tropical forests and large rivers transition into bays and canyons that may accumulate sunken vegetation. Figure B1 shows some of the diversity found on plant remains. *Adipicola longissima* (Figure B1 c) is a mussel found mainly in association with *Nypa fruticans* nuts. In contrast with other sunken wood mussels that have extensive geographic distributions in the Pacific, *Adipicola longissima* is restricted to the areas where nypa palms grow (mainly the Philippines, Indonesia, PNG, and the northern area of the Solomon Islands). Chitons revealed unsuspected diversity, and a wealth of undescribed species (Figure B1 a–f; Nicolas Puillandre, Muséum national d’Histoire naturelle, pers. comm., 2012). The amphipod genus *Bathyceradocus* (Maeridae; Figure B1 i) was represented by eight species, four of them new. A wood-based diet and the presence of

bacterial ectosymbiosis have been confirmed for several specimens, and molecular analyses revealed unexpectedly high diversity (recent work of author Corbari). Wood-dependent diets and bacterial interactions have already been demonstrated for different wood-associated organisms (sea urchins, Becker et al., 2009; *Pectinodonta*, Zbinden et al., 2010; Muniopsidae, Hoyoux et al., 2009). Future work will focus on placing trophic relationships in an evolutionary context.

Animals are not the only active decomposers of plant remains. Wood decay also results from the metabolic activities of bacteria (Waterbury et al., 1983; Distel and Roberts, 1997) and fungi (Ray, 1959; Ray and Stuntz, 1959). Although shallow marine fungi are common and diverse (550 species described, at least 1,500 expected to exist), deep-sea fungi appear to be rare (four species described from > 1,600 m) and are still little studied (Dupont et al., 2009, and references therein). For example, *Oceanitis scuticella*, originally described in 1977, was not seen until 2004, when specimens were collected in Vanuatu and the Solomon Islands during TDSB cruises (Dupont et al., 2009). *Alisea longicolla*, a new genus and species described from material collected alongside *O. scuticella* during a 2005 TDSB cruise (Dupont et al., 2009), is another example of how rare and understudied taxa are brought to light by the exploratory TDSB cruises. During BioPapua, deep-sea fungi were sampled at seven stations deeper than 700 m. Samples include a new occurrence for *O. scuticella* and also a new occurrence (at 700–1,150 m depth) of an undescribed morpho-species that was previously known from only a few specimens collected in 2007 off the Solomon Islands (Figure B1 g).

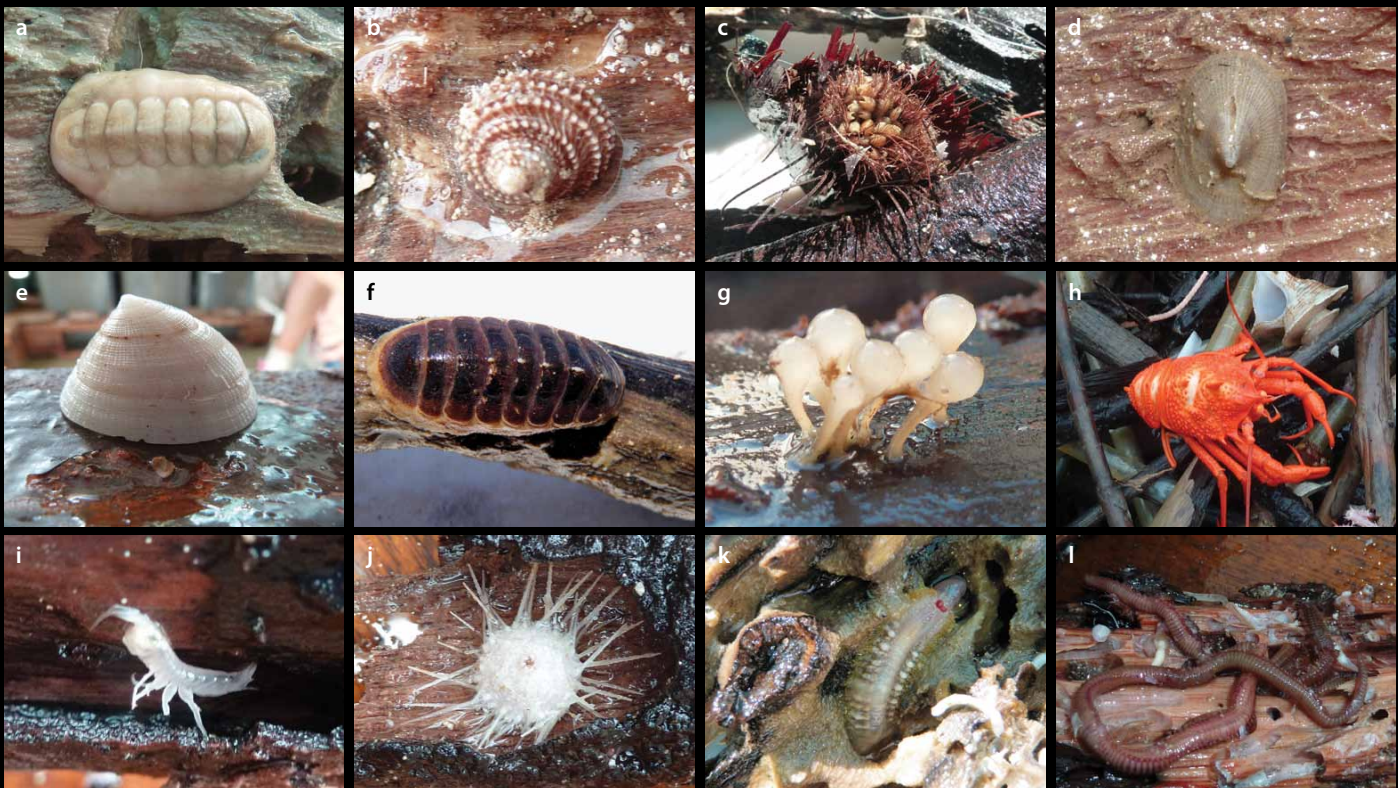


Figure B1. Deck photos of vegetation-associated fauna. (a) Chiton, *Ferreiraella* sp. (b) Cataegidae, *Cataegis* sp. (c) Mytilidae, *Adipicola longissima* nested in nypa palm nut. (d) Fissurellidae, *Puncturella* sp. (e) Pectinodontidae, *Pectinodonta* sp. (f) Chiton *Leptochiton* sp. (g) Undescribed fungi. (h) Muniopsidae *Galacantha* sp. (i) Maeridae, *Bathyceradocus* sp. (j) ?Echinidae. (k) Polynoidae, *Harmothoe* sp. (l) Eunicidae, *Eunice* sp.

samples collected during BioPapua into a larger study of the biogeography and integrative biology of *Adipicola iwaotakii*, a small bathymodioline mussel associated with sunken wood. This group has found high genetic diversity (seven mitochondrial COI haplotypes), a signal of population expansion, and a closer biogeographic relationship to the Solomon Islands, Vanuatu, and New Caledonia than to Japan and the Philippines. Among the 26 putative species of wood-associated mussels recognized by Lorion et al. (2010) for the Southwest Pacific, 11 were collected during BioPapua. None of the nine putative species found in the Philippines and Japan were collected in PNG; the wood-associated mussel fauna of PNG has therefore stronger affinities with southern locations such as New Caledonia.

Connectivity and Endemism of Seamount Fauna

Describing biodiversity from underwater mountains or seamounts (e.g., Stocks, 2009) has become one of the major themes of deep-sea exploration (e.g., special issue on “Mountains in the Sea,” *Oceanography* vol. 23, March 2010, <http://www.tos.org/oceanography/archive/23-1.html>). Seamounts are among the most ubiquitous underwater features in the ocean (Wessel et al., 2010) and may constitute one of the largest marine biomes, with a cumulative surface area exceeding 17 million km² (Etnoyer et al., 2010; Yesson et al., 2011).

Seamounts constitute an ideal system for the study of deep-sea biogeography as they are prevalent across ocean basins, are patches of hard substrata scattered on vast sedimentary plains, and are characterized by hydrographic

features that could significantly hinder faunal dispersal (e.g., Clark et al., 2010). The extent of faunal connectivity among seamounts and seamount chains is, however, still poorly known. Beyond theoretical inquiries, there is a strong practical need to understand seamount ecosystems in order to manage fragile fisheries resources and associated fauna. Seamounts aggregate commercially important fish species and are hotspots of pelagic and benthic biodiversity (Samadi et al., 2007b; Morato et al., 2010). The impact of deep-sea trawling on developing seamount fisheries has been shown to be catastrophic and long lasting (Althaus et al., 2009; Williams et al., 2010); therefore, there is no more critical time to study seamount ecosystems.

The scarcity of data on seamount fauna, however, prevents us from conceptualizing the processes that shape and maintain seamount faunal assemblages. The major obstacles to describing the biodiversity and biogeography of seamount fauna are (1) a lack of geographically comprehensive sampling, (2) the paucity of model systems allowing faunal comparisons across seamount chains, oceans, and depth regimes, and (3) the lack of integration of genetic information into the estimation of endemism levels. Indeed, since the inception of seamount science, many paradigms for the ecology of seamount fauna have been proposed, but few are strongly supported by empirical evidence (Rowden et al., 2010). There is therefore a strong need for the seamount research community to sample across the diversity of seamount environments (e.g., depth range, steepness, geological origin, habitat composition, and water-column

productivity) and geographical locations (e.g., latitude and isolation from continental margins).

One of the goals of BioPapua was to help fill the geographical gap in our understanding of Pacific seamount communities. Three of the seamounts catalogued by Allain et al. (2008) were sampled during BioPapua. Two are located in the Bismarck Sea, between Manus Island and the Western Rift accretion zone (3.05°S, 147.53°E and 3.23°S, 147.33°E, five stations sampled). The first seamount, Limana Kaia, appeared poor in benthic fauna, as our trawl mostly brought back bare rocks. This negative result might be explained by limited and/or unsuccessful sampling on rugged terrain. The second seamount, Mata Na Taru, is more interesting from a biological standpoint, as we were able to collect a diverse fauna. The third seamount (Sanguma, 5.53°S, 154°E, seven stations sampled) is located east of the north end of Bougainville Island, on the edge of the Solomon Trench, an active zone of subduction of the Solomon Plate under the Pacific Plate. This seamount, sampled at depths between 369 and 768 m, revealed a wealth of filter-feeding invertebrates, such as hydroids, sea pens, octocorals, and sea anemones, as well as a rich crustacean fauna.

Forty-four live specimens of *Nassaria* were collected during BioPapua, including seven on Sanguma Seamount. This neogastropod, with a nonplanktotrophic, poorly dispersive larval stage, is one of the model systems used to investigate faunal connectivity patterns between slope and seamount environments in New Caledonia (Castelin, 2010; Castelin et al., 2010). Among the 250 individuals previously analyzed (collected during

seven cruises representing approximately 800 sampling stations), 11 putative molecular species were detected, of which four were found exclusively in the Philippines (111 stations), and seven in New Caledonia (600 stations). Among the 44 BioPapua specimens of *Nassaria*, nine putative molecular species (one

common among BioPapua stations, all the others being rare) were detected, and only two of these are shared with the rich New Caledonian fauna (Magalie Castelin, Muséum national d'Histoire naturelle, *pers. comm.*, 2012).

Among octocorals, *Chrysogorgia* was particularly diverse, as 12 putative

species (based on DNA barcoding using *mtMutS*; McFadden et al., 2010; Pante and Watling, 2011) were detected, 25% of them new to our collections (Pante et al., 2012) and most being rare. This species pool represents 35% of the diversity found in the Pacific, and 27% of the total haplotypic richness of

BOX 2. BIODIVERSITY HIGHLIGHTS

One main focus of TDSB cruises is to explore and document deep-sea biodiversity. While searching for accumulations of sunken vegetation at the mouth of the Sepik River (03°53'S, 144°41'E), we sampled organisms typically found at cold seeps and hydrothermal vents, among them beard worms (Siboglinidae: *Escarpia* sp. and *Lamellibrachia* sp.) and two undescribed species of bathymodioline mussels (*Gigantidas* sp.; Figure B2 e–f), one of which associated with a polynoid scale worm (*Branchipolynoe* aff. *pettiboneae*; Figure B2 g). Several undescribed species of *Gigantidas* were already known from nearby seep localities (Kyuno et al., 2009) off New Guinea. On the last leg of BioPapua, we sampled the extraordinary copepod *Cardiodectes* sp. (Figure B2 i; Jean-Lou Justine, Muséum national d'Histoire naturelle, *pers. comm.*, 2012) on the eye of its fish host, and eulimid gastropods neatly attached on their urchin host (Figure B2 c). Species of the Eulimidae are all parasites of echinoderms, and much work remains to be done to understand patterns of host specificity and echinoderm-mollusk co-evolution. Another noteworthy find was a specimen of *Bayerotrochus* (Figure B2 a). This grazing mollusk of the family Pleurotomariidae has a continuous fossil record since the Silurian. As for many other groups, pleurotomariids had never before been recorded from the vicinity of New Guinea (Harasewych, 2002). This specimen probably belongs to an undescribed species (Patrick Anseeuw, Royal Belgian Institute of Natural Sciences, *pers. comm.*, 2012).

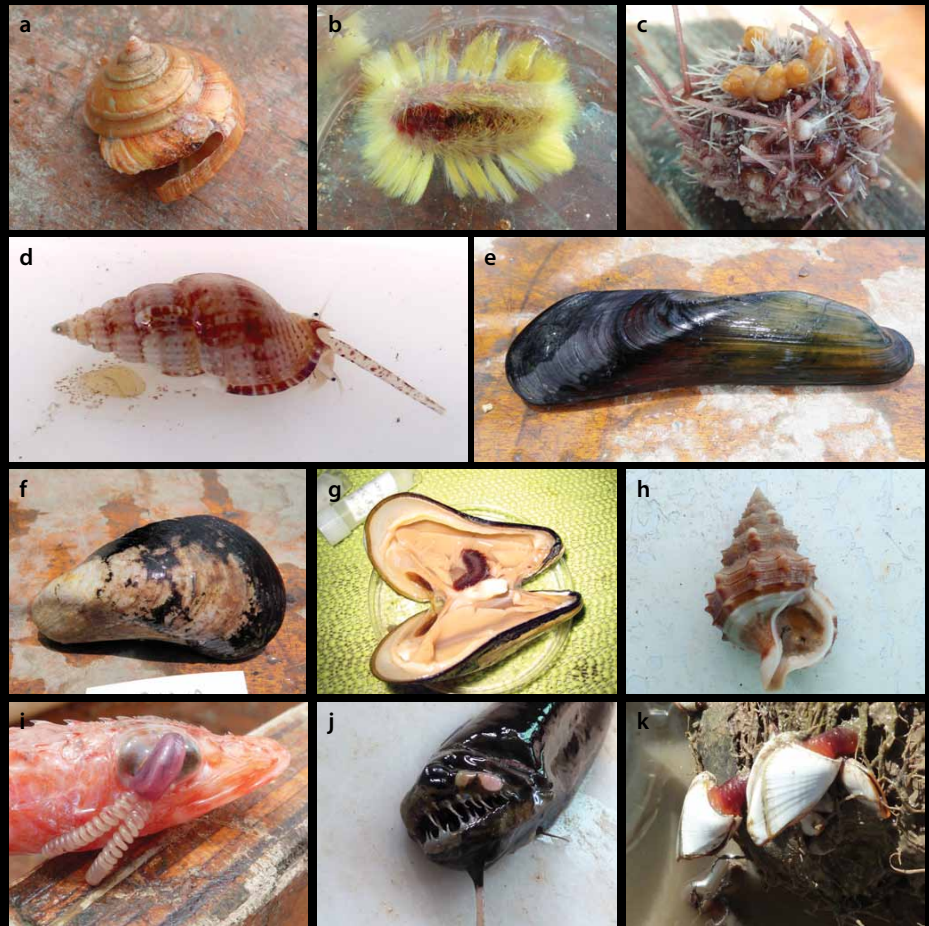


Figure B2. Biodiversity examples: (a) Pleurotomariidae, *Bayerotrochus* sp. (b) Amphinomidae, *Chloea* sp. (c) Eulimidae, *Pelseneeria* sp. on sea-urchin. (d) Nassariidae, *Nassarius* sp. (e) Mytilidae, *Gigantidas* sp. nov. 1. (f–g) Mytilidae, *Gigantidas* sp. nov. 2 in association with *Branchipolynoe* sp. nov. (h) Buccinidae, *Nassaria* sp. (i) Parasitic copepod Pennellidae, *Cardiodectes* sp. (j) Deep-sea fish, ?Chauliodidae. (k) Cirripedia, Lepadidae.

the genus (although we warn that these results will have to be analyzed using rarefaction analysis). Interestingly, two of these 12 putative species collected on Sanguma Seamount were also previously found on New Caledonian seamounts (one on Norfolk Ridge, the other on Loyalty Ridge), suggesting, as for the gastropod *Nassaria*, broad geographical distribution of these seamount organisms.

CONCLUSION

Very little is known of the biodiversity and biogeography of deep-sea animals from PNG. The data available, however, suggest that deep New Guinean fauna is at the confluence of significantly different biogeographic regions, and is more closely related to the southern than the northern Pacific fauna. Preliminary data suggest that deep New Guinean fauna is highly diversified. As an example, a rapid assessment of decapod crustacean biodiversity revealed more than 500 species collected, including four new genera (in the families Solenoceridae, Galatheidae, Callianassidae and Parapaguridae; Figure 4) and about 15% new species. We expect that further study of the material collected during BioPapua will shed light on large-scale biogeographic patterns in the tropical deep sea of the Western Pacific Ocean. While we are just beginning to fathom the amplitude of biodiversity in deep New Guinean waters, mining exploration and exploitation of seafloor massive sulfides (SMS) is flourishing in the region (Hoagland et al., 2010; Van Dover, 2011). The exploitation of metals from SMS deposits is an emerging industry, and adverse environmental effects are hard to predict, as hydrothermal vent and adjacent




Figure 4. New and undescribed crustacean species. (a–b) Family Solenoceridae, *Maximiliaeus odoceros* (newly described by Chan, 2012). (c) Family Epialtidae, *Oxypheurodon stimpsoni*. (d) Family Goneplacidae, *Thyraplax* sp. (e) Family Paguridae, *Bathypaguropsis* sp. (f) Family Munidopsidae, *Munidopsis* sp. Photos: Tin-Yam Chan

ecosystems are still poorly known. We therefore hope that our geographically comprehensive sampling program will provide a baseline for the biodiversity of the deep benthic organisms of the Bismarck and Solomon Seas.

ACKNOWLEDGEMENTS

The authors warmly thank the crew of R/V *Alis*, who made the TDSB cruise series a great success. We thank the participants of the BioPapua cruise: Jesse Apone, Edwin Sohun, and Alfred Ko'ou (UPNG); Julie Ponsard (University of Liège); Mao-Ying Lee and Rwei Yi Lee (National Taiwan Ocean University);

and Anders Warén (Swedish Museum of Natural History). We warmly thank our contacts at the University of Papua New Guinea and the PNG National Research Institute, particularly Jim Robins who was instrumental in obtaining research permits, and Edward Vanden Berghe and Gilberto Marani for their help extracting data from the OBIS database. We thank Nicolas Puillandre, Magalie Castelin, Stéphane Hourdez, Jean-Lou Justine, Patrick Anseeuw, and James Albert for sharing data and providing specimen identifications. Comments from Amélia Viricel and three anonymous reviewers significantly

improved the manuscript. EP thanks Estefania Rodriguez (American Museum of Natural History) and Scott France (University of Louisiana at Lafayette) for their financial support. The participation of TYC in the BioPapua cruise was supported by the Academia Sinica and the National Science Council, Taiwan R.O.C. The research on wood organisms is supported by the French “Fondation pour la Recherche en Biodiversité” (grant FRB2009 BioWood 340-10). 

REFERENCES

- Allain, V., J.-A. Kerandel, S. Andréfouët, F. Magron, M. Clark, D.S. Kirby, and F.E. Muller-Karger. 2008. Enhanced seamount location database for the western and central Pacific Ocean: Screening and cross-checking of 20 existing datasets. *Deep-Sea Research Part I* 55:1,035–1,047, <http://dx.doi.org/10.1016/j.dsr.2008.04.004>.
- Althaus, F., A. Williams, T.A. Schlacher, R.J. Kloser, M.A. Green, B.A. Barker, N.J. Bax, P. Brodie, and M.A. Schlacher-Hoenlinger. 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. *Marine Ecology Progress Series* 397:279–294, <http://dx.doi.org/10.3354/meps08248>.
- Auzende, J., J. Ishibashi, Y. Beaudoin, J. Charlou, J. Delteil, J. Donval, Y. Fouquet, J. Gouillou, B. Ildefonse, H. Kimura, and others. 2000. The eastern and western tips of Manus Basin (Papua, New Guinea) explored by submersible: MANAUTE cruise. *Comptes Rendus de l'Académie des Sciences, Série II, Sciences de la Terre et des Planètes* 331:119–126, [http://dx.doi.org/10.1016/S1251-8050\(00\)01387-2](http://dx.doi.org/10.1016/S1251-8050(00)01387-2).
- Bachraty, C., P. Legendre, and D. Desbruyères. 2009. Biogeographic relationships among deep-sea hydrothermal vent faunas at global scale. *Deep-Sea Research Part I* 56:1,371–1,378, <http://dx.doi.org/10.1016/j.dsr.2009.01.009>.
- Becker, P.T., S. Samadi, M. Zbinden, C. Hoyoux, P. Compère, and C. De Ridder. 2009. First insights into the gut microflora associated with an echinoid from wood falls environments. *Cahiers de Biologie Marine* 50:343–352, <http://hdl.handle.net/2268/77107>.
- Belyaev, G.M. 1972. *Hadal Bottom Fauna of the World Ocean*. Israel Program for Scientific Translations, Jerusalem, 199 pp. [Translated from Russian]
- Both, R., K. Crook, B. Taylor, S. Brogan, B. Chappell, E. Frankel, L. Liu, J. Sinton, and D. Tiffin. 1986. Hydrothermal chimneys and associated fauna in the Manus back-arc basin, Papua New Guinea. *Eos, Transactions American Geophysical Union* 67:489–490, <http://dx.doi.org/10.1029/EO0671021p00489>.
- Bouchet, P., V. Héros, P. Lozouet, and P. Maestrati. 2008. A quarter-century of deep-sea malacological exploration in the South and West Pacific: Where do we stand? How far to go? Pp. 9–40 in *Tropical Deep-Sea Benthos* 25. V. Héros, R.H. Cowie, and P. Bouchet, eds, *Mémoires du Muséum national d'Histoire naturelle*, vol. 196.
- Castelin, M. 2010. Lien entre endémisme et développement larvaire en milieu marin. Le cas des gastéropodes des monts sous-marins de la Zone Economique Exclusive de Nouvelle Calédonie. PhD dissertation, Muséum national d'Histoire naturelle, Paris.
- Castelin, M., J. Lambourdière, M. Boisselier, P. Lozouet, A. Couloux, C. Cruaud, and S. Samadi. 2010. Hidden diversity and endemism on seamounts: Focus on poorly dispersive neogastropods. *Biological Journal of the Linnean Society* 100:420–438, <http://dx.doi.org/10.1111/j.1095-8312.2010.01424.x>.
- Chan, T.Y. 2012. A new genus of deep-sea sole-nocericid shrimp (Decapoda: Penaeoidea) from Papua New Guinea. *Journal of Crustacean Biology* 32:489–495.
- Clark, M.R., A.A. Rowden, T. Schlacher, A. Williams, M. Conalvey, K.I. Stocks, A.D. Rogers, T.D. O'Hara, M. White, T.M. Shank, and J.M. Hall-Spencer. 2010. The ecology of seamounts: Structure, function, and human impacts. *Annual Review of Marine Science* 2:253–278, <http://dx.doi.org/10.1146/annurev-marine-120308-081109>.
- Desbruyères, D., J. Hashimoto, and M.-C. Fabri. 2006. Composition and biogeography of hydrothermal vent communities in western Pacific back-arc basins. Pp. 215–234 in *Geophysical Monograph Series*, vol. 166. D.M. Christie, C.R. Fisher, S.-M. Lee, and S. Givens, eds, American Geophysical Union, <http://dx.doi.org/10.1029/166GM11>.
- Diamond, J.M. 1972. Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences of the United States of America* 69:3,199–3,203.
- Diamond, J.M. 1973. Distributional ecology of New Guinea birds: Recent ecological and biogeographical theories can be tested on the bird communities of New Guinea. *Science* 179:759–769, <http://dx.doi.org/10.1126/science.179.4075.759>.
- Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129–146, [http://dx.doi.org/10.1016/0006-3207\(75\)90052-X](http://dx.doi.org/10.1016/0006-3207(75)90052-X).
- Distel, D., A.R. Baco, E. Chuang, W. Morrill, C. Cavanaugh, and C.R. Smith. 2000. Marine ecology: Do mussels take wooden steps to deep-sea vents? *Nature* 403:725–726, <http://dx.doi.org/10.1038/35001667>.
- Distel, D., and S. Roberts. 1997. Bacterial endosymbionts in the gills of the deep-sea wood-boring bivalves *Xylophaga atlantica* and *Xylophaga washingtona*. *Biological Bulletin* 192:253–261.
- Dupont, J., S. Magnin, F. Rousseau, M. Zbinden, G. Frebourg, S. Samadi, B. Richer de Forges, and E.B.G. Jones. 2009. Molecular and ultrastructural characterization of two ascomycetes found on sunken wood off Vanuatu Islands in the deep Pacific Ocean. *Mycological Research* 113:1,351–1,364, <http://dx.doi.org/10.1016/j.mycres.2009.08.015>.
- Etnoyer, P., J. Wood, and T. Shirley. 2010. How large is the seamount biome? *Oceanography* 23(1):206–209, <http://dx.doi.org/10.5670/oceanog.2010.96>.
- Flannery, T. 1998. *Throwim Way Leg: Tree-kangaroos, Possums, and Pennis Gourds: On the Track of Unknown Mammals in Wildest New Guinea*. Grove Press, New York, 327 pp.
- Hall, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: Computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20:353–431, [http://dx.doi.org/10.1016/S1367-9120\(01\)00069-4](http://dx.doi.org/10.1016/S1367-9120(01)00069-4).
- Hamilton, A.J., Y. Basset, K.K. Benke, P.S. Grimbacher, S.E. Miller, V. Novotný, G.A. Samuelson, N.E. Stork, G.D. Weiblen, and J.D.L. Yen. 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. *The American Naturalist* 176:90–95, <http://dx.doi.org/10.1086/652998>.
- Hessler, R.R., and P.F. Lonsdale. 1991. Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Research Part A* 38:185–199, [http://dx.doi.org/10.1016/0198-0149\(91\)90079-U](http://dx.doi.org/10.1016/0198-0149(91)90079-U).
- Hoagland, P., S. Beaulieu, M.A. Tivey, R.G. Eggert, C. German, L. Glowka, and J. Lin. 2010. Deep-sea mining of seafloor massive sulfides. *Marine Policy* 34:728–732, <http://dx.doi.org/10.1016/j.marpol.2009.12.001>.
- Hoyoux, C., M. Zbinden, S. Samadi, F. Gaill, and P. Compère. 2009. Wood-based diet and gut microflora of a galatheid crab associated with Pacific deep-sea wood falls. *Marine Biology* 156:2,421–2,439, <http://dx.doi.org/10.1007/s00227-009-1266-2>.
- Kyuno, A., M. Shintaku, Y. Fujita, H. Matsumoto, M. Utsumi, H. Watanabe, Y. Fujiwara, and J.-I. Miyazaki. 2009. Dispersal and differentiation of deep-sea mussels of the genus *Bathymodiolus* (Mytilidae, Bathymodiolinae). *Journal of Marine Biology* Article ID 625672, 15 pp., <http://dx.doi.org/10.1155/2009/625672>.
- Lisitsyn, A.P., K.A.W. Crook, Y.A. Bogdanov, L.P. Zonenshayn, K.G. Murav'ev, W. Tufar, Y.G. Gurvich, V.V. Gordeyev, and G.V. Ivanov. 1993. A hydrothermal field in the rift zone of the Manus Basin, Bismarck Sea. *International Geology Review* 35:105–126, <http://dx.doi.org/10.1080/00206819309465517>.

- Lonsdale, P. 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research* 24:857–858, [http://dx.doi.org/10.1016/0146-6291\(77\)90478-7](http://dx.doi.org/10.1016/0146-6291(77)90478-7).
- Lorion, J., B. Buge, C. Cruaud, and S. Samadi. 2010. New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia). *Molecular Phylogenetics and Evolution* 57:71–83, <http://dx.doi.org/10.1016/j.ympev.2010.05.027>.
- Lorion, J., S. Duperron, O. Gros, C. Cruaud, and S. Samadi. 2009. Several deep-sea mussels and their associated symbionts are able to live both on wood and on whale falls. *Proceedings of the Royal Society of London Series B* 275:177–185, <http://dx.doi.org/10.1098/rspb.2008.1101>.
- Lorion, J., and S. Samadi. 2010. Species richness, sampling bias and phylogenetics in deep-sea mussels. *Cahiers de Biologie Marine* 51:435–439.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, 203 pp.
- Macpherson, E., B. Richer de Forges, K. Schnabel, S. Samadi, M.-C. Boisselier, and A. Garcia-Rubies. 2010. Biogeography of the deep-sea galatheid squat lobsters of the Pacific Ocean. *Deep-Sea Research Part I* 57:228–238, <http://dx.doi.org/10.1016/j.dsr.2009.11.002>.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York, NY, 334 pp.
- Morato, T., S.D. Hoyle, V. Allain, and S.J. Nicol. 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences of the United States of America* 107:9,707–9,711, <http://dx.doi.org/10.1073/pnas.0910290107>.
- Novotný, V., Y. Basset, S.E. Miller, G.D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* 416:841–844, <http://dx.doi.org/10.1038/416841a>.
- Pante, E., S.C. France, A. Couloux, C. Cruaud, C.S. McFadden, S. Samadi, L. Watling. 2012. Deep-sea origin and in-situ diversification of chrysogorgiid octocorals. *PLoS ONE* 7(6):e38357, <http://dx.doi.org/10.1371/journal.pone.0038357>.
- Puillandre, N., A.V. Sysoev, B.M. Olivera, A. Couloux, and P. Bouchet. 2010. Loss of planktotrophy and speciation: Geographical fragmentation in the deep-water gastropod genus *Bathytoma* (Gastropoda, Conoidea) in the western Pacific. *Systematics and Biodiversity* 8:371–394, <http://dx.doi.org/10.1080/14772001003748709>.
- Ray, D. 1959. Marine fungi and wood borer attack. *Proceedings of the American Wood Preservers Association* 55:1–7.
- Ray, D., and D. Stuntz. 1959. Possible relation between marine fungi and *Limnoria* on submerged wood. *Science* 129:93–94, <http://dx.doi.org/10.1126/science.129.3341.93>.
- Richer de Forges, B., and L. Corbari. 2012. A new species of *Oxypleurodon* Miers, 1886 (Crustacea, Brachyura, Majoidea) from the Bismarck Sea, Papua New Guinea. *Zootaxa* 3320:56–60.
- Rowden, A.A., J.F. Dower, T.A. Schlacher, M. Consalvey, and M.R. Clark. 2010. Paradigms in seamount ecology: Fact, fiction and future. *Marine Ecology* 31:226–241, <http://dx.doi.org/10.1111/j.1439-0485.2010.00400.x>.
- Samadi, S., E. Quéméré, J. Lorion, A. Tillier, R. von Cosel, P. Lopez, C. Cruaud, A. Couloux, and M. Boisselier-Dubayle. 2007a. Molecular phylogeny in mytilids supports the wooden steps to deep-sea vents hypothesis. *Comptes Rendus Biologies* 330:446–456, <http://dx.doi.org/10.1016/j.crv.2007.04.001>.
- Samadi, S., T. Schlacher, and B. Richer de Forges. 2007b. Seamount benthos. Pp. 117–140 in *Seamounts: Ecology, Fisheries & Conservation*. T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N. Haggan, and R.S. Santos, eds, Blackwell Publishing Ltd., Oxford, UK, <http://dx.doi.org/10.1002/9780470691953.ch7>.
- Samadi, S., L. Corbari, J. Lorion, S. Hourdez, T. Haga, J. Dupont, M.-C. Boisselier, and B. Richer de Forges. 2010. Biodiversity of deep-sea organisms associated with sunken-wood or other organic remains sampled in the tropical Indo-Pacific. *Cahiers de Biologie Marine* 51:459–466.
- Stocks, K. 2009. *SeamountsOnline: An Online Information System for Seamount Biology*. Available online at <http://seamounts.sdsc.edu> (accessed June 20, 2011).
- Tregoning, P., H. McQueen, K. Lambeck, R. Jackson, R. Little, S. Saunders, and R. Rosa. 2000. Present-day crustal motion in Papua New Guinea. *Earth Planets and Space* 52:727–730.
- Tufar, W. 1990. Modern hydrothermal activity, formation of complex massive sulfide deposits and associated vent communities in the Manus back-arc basin (Bismarck Sea, Papua New Guinea). *Mitteilung der Osterreichischen Geologischen Gesellschaft* 82:183–210.
- Tyler, P., and C. Young. 2003. Dispersal at hydrothermal vents: A summary of recent progress. *Hydrobiologia* 503:9–19, <http://dx.doi.org/10.1023/B:HYDR.0000008492.53394.6b>.
- Vanden Berghe, E., ed. 2007. *The Ocean Biogeographic Information System: Web Pages*, <http://www.iobis.org> (accessed August 12, 2011).
- Van Dover, C. 2011. Mining seafloor massive sulphides and biodiversity: What is at risk? *ICES Journal of Marine Science* 68:341–348, <http://dx.doi.org/10.1093/icesjms/fsq086>.
- Van Dover, C., C. German, K. Speer, L. Parson, and R. Vrijenhoek. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295:1,253–1,257, <http://dx.doi.org/10.1126/science.1067361>.
- Veron, J.E.N., L.M. Devantier, E. Turak, A.L. Green, S. Kininmonth, M. Stafford-Smith, and N. Peterson. 2009. Delineating the Coral Triangle. *Galaxea, Journal of Coral Reef Studies* 11:91–100.
- Vrijenhoek, R.C. 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19:4,391–4,411, <http://dx.doi.org/10.1111/j.1365-294X.2010.04789.x>.
- Wallace, A. 1869. *The Malay Archipelago: The Land of the Orang Utan, and the Bird of Paradise*. Harper & Brothers, New York, 638 pp.
- Wallace, A. 1876. *The Geographical Distribution of Animals*. Macmillan, London, 607 pp.
- Warén, A. 2011. Molluscs on biogenic substrates. Pp. 438–448 in *The Natural History of Santo*. P. Bouchet, H. Le Guyader, and O. Pascal, eds, *Patrimoines Naturels*, vol. 70, Muséum national d'Histoire naturelle, Paris, France.
- Waterbury, J., C. Calloway, and R. Turner. 1983. A cellulolytic-nitrogen fixing bacterium cultured from the gland of Deshayes in shipworms. *Science* 221:1,401–1,403, <http://dx.doi.org/10.1126/science.221.4618.1401>.
- Watling, L., S.C. France, E. Pante, and A. Simpson. 2011. Biology of deep-water octocorals. *Advances in Marine Biology* 60:41–123, <http://dx.doi.org/10.1016/B978-0-12-385529-9.00002-0>.
- Wessel, P., D.T. Sandwell, and S.S. Kim. 2010. The global seamount census. *Oceanography* 23(1):24–33, <http://dx.doi.org/10.5670/oceanog.2010.60>.
- Williams, A., T.A. Schlacher, A.A. Rowden, F. Althaus, M.R. Clark, D.A. Bowden, R. Stewart, N.J. Bax, M. Consalvey, and R.J. Kloser. 2010. Seamount megabenthic assemblages fail to recover from trawling impacts. *Marine Ecology* 31:183–199, <http://dx.doi.org/10.1111/j.1439-0485.2010.00385.x>.
- Wolff, T. 1979. Macrofaunal utilization of plant remains in the deep-sea. *Sarsia* 64:117–136.
- Yesson, C., M.R. Clark, M.L. Taylor, and A.D. Rogers. 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep-Sea Research Part I* 58:442–453, <http://dx.doi.org/10.1016/j.dsr.2011.02.004>.
- Zbinden, M., M. Pailleret, J. Ravaux, S.M. Gaudron, C. Hoyoux, J. Lambourdière, A. Warén, J. Lorion, S. Halary, and S. Duperron. 2010. Bacterial communities associated with the wood-feeding gastropod *Pectinodonta* sp. (Patellogastropoda, Mollusca). *FEMS Microbiology Ecology* 74:450–463, <http://dx.doi.org/10.1111/j.1574-6941.2010.00959.x>.