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RESEARCH ARTICLE

Sarah Samadi · Lionel Bottan · Enrique Macpherson
Bertrand Richer De Forges · Marie-Catherine Boisselier

Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates

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Abstract Previous studies have suggested that the high diversity associated with the Norfolk seamounts (Southwest Pacific) could reflect endemism resulting from limited dispersal due to hydrological phenomena. Crustaceans of the family Galatheidae are thoroughly studied in the New Caledonia economic zone permitting the analysis of species distribution pattern between the New Caledonia slope and Norfolk ridge seamounts. This analysis has shown that, qualitatively, the same species are sampled on seamounts and on the New Caledonia slope. Local endemism was never detected. However, on each seamount, and therefore on a small surface, a very high number of species are usually sampled, suggesting that seamounts are biodiversity hot spots. Then, to evaluate whether the seamounts constitute patches of isolated habitat, we explore the pattern of genetic diversity within several species of crustaceans and gastropods. Analysis of the intra-specific genetic structure using the mitochondrial marker COI reveals that populations of two Galatheidae species (*Munida thoe* and *Munida zebra*), polymorphic for this marker, are genetically not structured, both among seamounts and between the seamounts and the island slope. The genetic structure over a similar sampling scheme of two *Eumunida* species (Chirostylidae, the sister family of Galatheidae) and a planktotrophic gastropod (*Sassia remensa*) reveals a similar pattern. Population structure is observed only in *Nassaria problematica*, a non-planktotrophic gastropod with limited larvae dispersal. Thus, the limitation of gene flow between seamounts appears to be observed only for species with limited dispersal abilities. Our results suggest that the Norfolk seamounts rather than functioning as areas of endemism, instead, may be highly productive zones that can support numerous species in small areas.

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S. Samadi (✉) · L. Bottan · B. R. De Forges · M.-C. Boisselier
"Systématique, Adaptation et Evolution",
UR IRD 148 /UMR 7138 UPMC; IRD; MNHN; CNRS,
Service de systématique moléculaire (CNRS, IFR101),
Département Systématique et Evolution,
Muséum National d'Histoire Naturelle, CP 26,
57 Rue Cuvier, 75231 Paris Cedex 05, France
E-mail: sarah@mnhn.fr
Tel.: +33-1-40793759
Fax: +33-1-40793844

E. Macpherson · B. R. De Forges
Centro de Estudios Avanzados de Blanes (CSIC),
C. acc. Cala Sant Francesc 14, 17300 Blanes, Girona, Spain

B. R. De Forges
"Systématique, Adaptation et Evolution",
UMR 7138 UPMC-IRD-MNHN-CNRS (UR IRD 148),
Institut de Recherche pour le Développement, B.P. A5,
98848 Nouméa Cedex, Nouvelle-Calédonie, France

Introduction

The endemism and species richness, which have been abundantly documented in the terrestrial biota of oceanic islands, are often explained by the acceleration of evolutionary processes due to the fragmentation of species into small isolated populations (Barton 1998). Oceanic water masses are, in this context, seen as physical barriers between small patches of land each occupied by a patch of terrestrial organisms isolated from other patches. An analogy has often been proposed between oceanic islands and similar topographical features such as mountains on land, and underwater seamounts in the marine realm. The background hypothesis supporting these analogies is that environmental discontinuity between prominent topographic features is a barrier to dispersal and thus causes fragmentation into small isolated sub-populations. In the case of mountain summits, the analogy is often supported by the high endemism rates observed. Mountain summits are physically separated by low areas that differ by environmental parameters. Organisms are not supposed to be simultaneously adapted to these contrasted environmental conditions. Thus, this environmental discontinuity is supposed to reduce dispersal from one summit

to another. Similarly, to explain the diversity and apparent endemism of the benthic seamount fauna of the southwest Pacific, it has been hypothesized that seamounts can induce similar isolation between small populations under the sea (Richer de Forges et al. 2000). In the study of Richer de Forges et al. (2000), 36% of fish and macro-invertebrate species were new to science and thus never sampled from the open seafloor and closest continental slopes. Moreover, very low species overlap was observed between samples from seamounts separated by only a few kilometres. These observations were interpreted as an indication of high endemism rates on these seamounts, thus supporting the analogy between seamounts and terrestrial islands. More precisely, to explain the apparent endemism and low species overlap between seamounts, Richer de Forges et al. (2000) hypothesized that larval dispersal was limited by hydrological phenomena such as Taylor columns (Roden 1987), which result from the interaction between water circulation and topography, promoting larval retention and aggregation (Boehlert and Mundy 1993; Mullineaux and Mills 1996; Rogers 1994). This phenomenon could limit the efficiency of larval dispersion for organisms inhabiting seamounts, thus inducing isolation and permitting subsequent speciation.

However, the few genetic studies available for species associated with seamounts do not support population isolation at a local scale. For example, Aboim et al. (2005), using two mitochondrial genes, demonstrated that the populations of the benthopelagic fish *Helicolenus dactylopterus*, sampled on seamounts separated by a few hundreds of kilometres, were not differentiated. In this study, a genetic differentiation between populations was found only at larger oceanic scales (transatlantic). However, using micro-satellite loci, Aboim (2005) revealed that these seamounts populations were differentiated from a population sampled on the continental slope, about 2,000 km apart. Although most of the available genetic studies concerned fishes (reviewed in Creasey and Rogers 1999), some studies on benthic organisms over seamounts have suggested the same trend (see for example Smith et al. 2004).

In the marine realm high faunal similarities have, however, been observed between sites 3,000 and 4,000 km apart in other isolated deep-sea environments such as hydrothermal vent or cold seeps. Among vent organisms, recent population genetic studies of bivalves from the genus *Bathymodiolus* indicate dispersal between very distant sites (Won et al. 2003), and even between hydrothermal and cold-seep sites (Miyazaki et al. 2004). These results suggest that although vent and cold-seep environments are markedly fragmented, species associated with these environments can be highly dispersive. Thus, such environments are more like oases, i.e. places where a high trophic input allows abundance of species and high population density, than like islands, i.e. isolated patches of habitat that can accommodate only small populations of a few species without exchange with other such populations.

In contrast to the hypothesized isolation of seamount populations by Taylor columns, 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 up nutrients in the euphotic zone (Worm et al. 2003; Genin 2004). Thus, by analogy with deep-sea oases, an alternative hypothesis suggests that seamounts are highly productive oases that can accommodate dense populations of many species in small areas without isolation between population patches. Following this hypothesis, the low species overlap observed between seamounts and the surrounding open sea or continental slopes—i.e. the apparent high rate of endemism—may be explained by insufficient sampling due to differences in population density and local species abundances between these environments.

The first step to determine which of the insular isolation versus the oases models is the best to explain seamount biodiversity is to test whether the endemism described on seamounts is not an artefactual observation due to (a) a more intensive sampling on seamounts than on surrounding open sea floors and nearby continental slopes and/or (b) the concentration of numerous species on small seamounts areas that quantitatively increases sampling success for a given effort on seamounts as compared to these others areas, and/or (c) a poor taxonomic background that compromises the assessment of species distribution areas. We thus sought taxa for which taxonomical data are available and where the analyses of genetic structure among populations were possible in order to evaluate dispersal, and thus to find the best fitting hypothesis. Among the organisms found on the seamounts of the Norfolk ridge, the squat lobsters of the families Galatheidae and Chirostylidae are highly diversified. These families, which have been thoroughly studied in the New Caledonia economic zone (de Saint Laurent and Macpherson 1990; Macpherson 1993, 1994; Baba and de Saint Laurent 1996; Machordom and Macpherson 2004; Macpherson and Machordom 2005), were here used to evaluate the pattern of specific diversity over these seamounts.

Using five squat lobster species, we have first tested whether the association between topography and hydrological phenomena in the seamounts of Norfolk ridge leads to population fragmentation. This was done to test whether population fragmentation and subsequent genetic differentiation can induce high rates of speciation, which could account for the high species diversity observed. Towards this aim, the genetic variability of three Galatheidae species belonging to the genus *Munida* was analysed using mtDNA sequences from individuals collected on several seamounts on the Norfolk ridge. The results were compared to the population structure observed for two species of the genus *Eumunida* [family Chirostylidae, which is considered as the sister group of the family Galatheidae (Morrison et al. 2002)].

Although the taxonomic knowledge was important on this group, very poor data about the larval life history traits of squat lobsters and their dispersal capabilities were available. In order to evaluate the potential role of larval dispersal on genetic isolation between seamounts, two gastropod species with contrasting larval development were also surveyed. In Gastropods, larval development, which is easily determined by examining the protoconch, is highly correlated to dispersal abilities of larvae and thus, at least at local geographic scale, to population structure (Collins 2001; Kyle and Boulding 2000; Boisselier-Dubayle and Gofas 1999; Todd et al. 1998). If the association of topography and hydrological phenomena in Norfolk ridge seamounts leads to a physical fragmentation of seamount habitat, we would expect all the analysed species to be more or less genetically structured. Conversely, if there is no larval retention, we would expect only species with poorly dispersive larvae to be structured. Finally, by comparing results from such ecologically and phylogenetically distant taxa as gastropods and squat lobsters, we will discuss which of the two models (insular isolation vs oasis model), better explains species richness on South Pacific seamounts.

Seamounts are also important fishery resources, and Koslow et al. (2001) showed that on Tasmanian seamounts intensive fishery activities developed to catch orange roughy (*Hoplostethus atlanticus*) had drastically reduced the invertebrate biomass and thus possibly the biodiversity. Indeed, the biomass was 83% lower between heavily trawled seamounts (>1,000 trawls) and those of lightly fished (10–100 trawls). Although the high level of apparent endemism associated with seamounts has to be tempered against limited collections and poorly known systematics (Richer de Forges et al. 2000), seamounts have been suggested as a target for marine biodiversity protection (Richer de Forges and Chauvin 2005). In a biological conservation perspective, it is thus quite important to know whether their richness results from endemism or from the concentration of populations belonging to numerous widespread species. In both cases, the protection of limited areas will preserve the habitat of many species, but in the first instance (insular isolation model), rare endemic species would be protected, while in the second case (oasis model) protection would be provided to widespread species in a minimal surface.

Materials and methods

The fauna of Norfolk ridge seamounts was sampled by dredging and trawling during two cruises of R/V Alis. During the first cruise (NORFOLK1, June 2001), 9 seamounts and the "Isle des Pins" slope were explored, and during the second cruise (NORFOLK2, October 2003) 13 seamounts along with all sites explored during the previous cruise were sampled (Fig. 1). All specimens belonging to the Galatheidae and specimens of the genus *Eumunida* (Chirostylidae) were identified to species level and stored in 70° ethanol. All the materials of the present study are conserved in the Muséum National d'Histoire Naturelle, Paris.

For Galatheidae, the species accumulation curve over the 229 stations sampled during the two NORFOLK cruises was calculated using EstimateS 7.5 (Colwell 2005). We estimated the species richness using the Michaelis–Menten asymptotic function (Colwell and Coddington 1994) on species accumulation curves obtained through 50 random drawing of the 229 stations using the Bootstrap estimator and the first- and second-order Jackknife estimators.

In order to evaluate whether seamounts induce population fragmentation, we selected three species of *Munida* (*M. acantha, M. thoe* and *M. zebra*) and two species of *Eumunida* (*E. annulosa* and *E. sternomaculata*). Finally, to evaluate the potential role of larval dispersal on population structure, two gastropod species, sampled on most of the seamounts, but which differ in their larval development, were chosen. These were *Sassia remensa* (Ranellidae), which has a planktotrophic protoconch, suggesting high larvae dispersal abilities, and *Nassaria problematica* (Buccinidae) whose protoconch has non-planktotrophic characteristics suggesting an almost direct larvae development and thus limited dispersal ability.

In each selected species we analysed about four specimens per seamount (Table 3). The sampling scheme was supplemented whenever possible by specimens collected during previous cruises on the same seamounts and stored at the MNHN in Paris. A previously collected specimen of *M. thoe* from Wallis and Futuna (North East Fiji Island) was also analysed.

In both galatheids and gastropods, DNA was isolated from muscle tissue and purified using the DNeasy® 96 Tissue Kit (Qiagen) following the manufacturer's instructions and then stored at −20°C. The *cytochrome oxidase I* (COI) mitochondrial gene was amplified, using universal primers LCO1490 (5′-GGTCAACAAATCA TAAAGATATTGG-3′) and HCO2198 (5′-TAAACT TCAGG GTGACCAAAAAATCA-3′) developed by Folmer et al. (1994). PCR reactions were performed in 30 µl final volume, containing approximately 3 ng template DNA, 2.5 mM $MgCl_2$, 0.26 mM of each nucleotide, 0.3 µM of each primer, 5% DMSO and 1.5 unit of *Taq* Polymerase (Qbiogene). Amplification products were generated by an initial denaturation step of 4 min at 94°C followed by 40 cycles at 94°C for 30 s, 50°C for 30 s and 40 s at 72°C and by a final extension at 72°C for 5 min. PCR products were purified using Montage™ PCR Centrifugal Filter Devices (Millipore) and sequenced (Sanger et al. 1977) on a Ceq2000™ automated sequencer (Beckman), in both directions to confirm accuracy of each haplotype sequence.

Before analysing the pattern of genetic diversity, we evaluated whether observed sequence identity could be interpreted as identity by descent. Indeed, if the analysed sequence is saturated, an identical but homoplastic

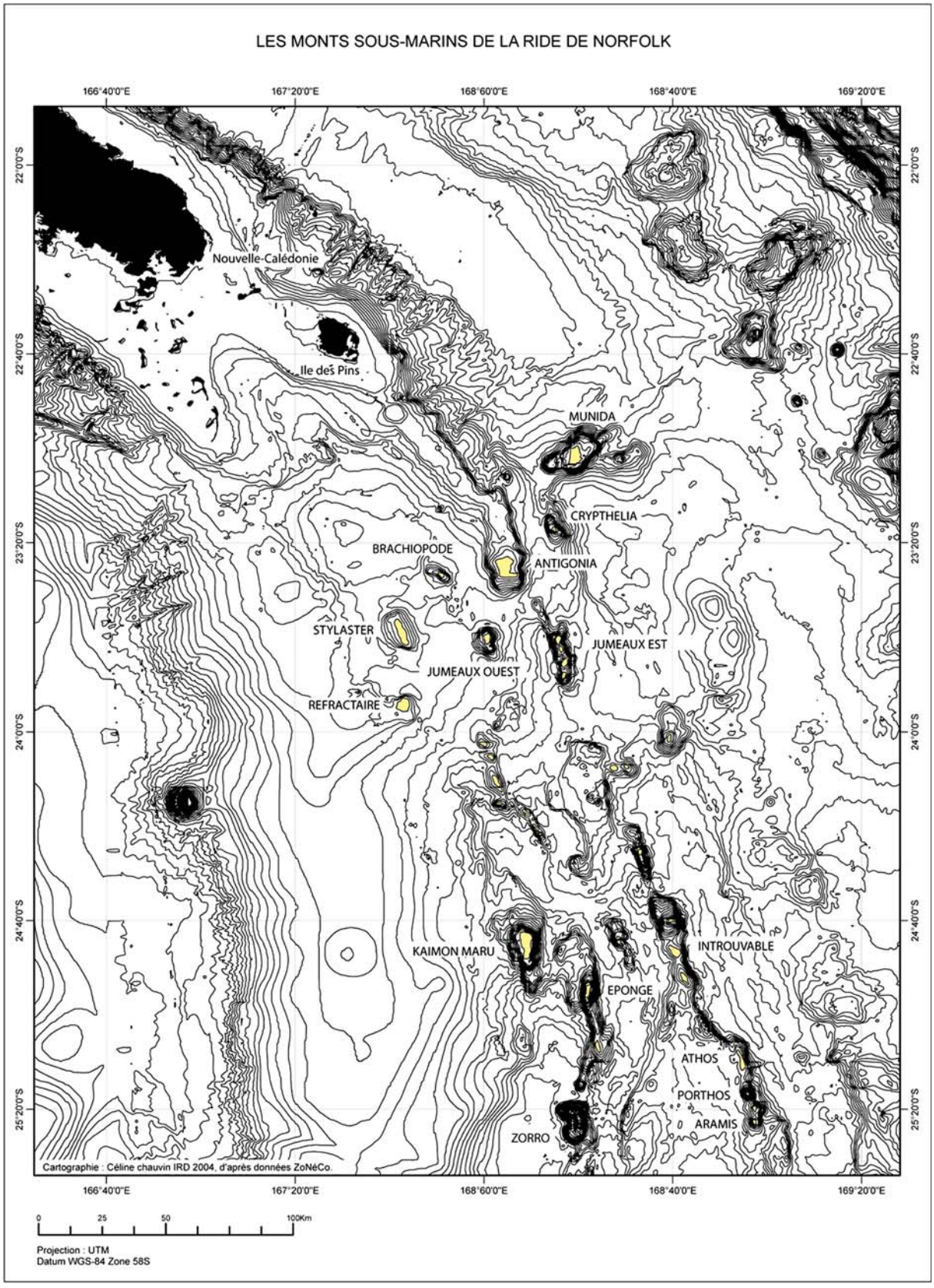

Fig. 1 Bathymetric map of the Caledonian part of the Norfolk ridge and the name given to the explored seamounts. *Northern area* Antigonia, Brachiopode, Crypthelia, Jumeau est, Jumeau ouest, Munida, Réfractaire, Stylaster. *Southern area* Aramis, Athos, Eponge, Introuvable, Kaimon Maru, Zorro

sequence could be found in two or more isolated population that in fact do not exchange genes. We thus performed a saturation analysis. Patristic and observed substitutions matrices were computed as described by Hassanin et al. (1998), using PAUP version 3.1.1 (Swofford 1993).

Within each species, analyses of molecular data were conducted using ARLEQUIN 2.0 software (Schneider et al. 2000). We first evaluated intra-specific genetic diversity by computing the number of haplotypes, the number of polymorphic sites, haplotype diversity (h)—i.e. the probability that two randomly selected haplotypes are different (Nei 1987)—and nucleotide sequence diversity (π)—i.e. the probability that two randomly selected homologous nucleotides differ (Tajima 1983; Nei 1987).

Second, within each species a genetic distance matrix between haplotypes was calculated using the Tamura–Nei method (Tamura and Nei 1993), which was used to draw the corresponding minimum spanning networks (MSNs) that allowed the visualization of the genealogical relations between haplotypes and their geographic distribution on the seamounts.

Third, we tested the correlation between the matrix of genetic distances between individuals, using Tamura–Nei genetic distance, and the geographical distances using the Mantel test (Mantel 1967), as implemented in ARLEQUIN.

Fourth, intra-species population genetic structure was tested by analysing molecular variance (AMOVA) at two hierarchical levels, i.e. between and within seamounts. Only seamounts for which sequence data were available for two or more individuals of the same species were included. With haploid data (haplotypes) and individuals grouped in local populations (i.e. by the seamount on which they were sampled), the implemented form of the algorithm led to a fixation index F_{ST} that is identical to the weighted average F statistics over loci defined by Weir and Cockerham (1984). The null distribution of F_{ST}, which permits inference of the P value of the estimated F_{ST}, was obtained by 10,000 permutations of the haplotypes among seamounts (Excoffier et al. 1992).

Finally, within each species we also investigated using the analysis of mismatch distributions of pairwise differences between all individuals, implemented in Arlequin version 2.000 software package (Schneider et al. 2000) the demographic history. This analysis allows the testing of whether a population has undergone a rapid population expansion or has remained stable over time (Aboim et al. 2005). We also used Arlequin to test within each species for departures from mutation-drift equilibrium with Tajima's D test (Tajima 1989). Because of small sampling size for each species, all populations from the same sampling date (same cruise) were pooled in a single group.

Results

Taxonomic diversity of South Pacific Galatheidae

Sixty-two of the 160 known species of Galatheidae (genera *Galathea* and *Munidopsis* excluded) from the SW Pacific Ocean were identified over the 229 stations explored during the two NORFOLK cruises. Our sampling included 42% of the Galatheidae diversity known in the South Pacific (Tables 1, 2) from Norfolk

Table 1 Geographical distribution of species richness (number of species sampled) of Galatheidae genera and *Eumunida* (Chirostylidae) on Norfolk ridge seamounts

		Depth (m)			Number of stations sampled	Galatheidae				*Eumunida spp.*
		Min	Max	Mean		*Agononida spp.*	*Munida spp.*	*Paramunida spp.*	Other genera (pooled)	
"Isle des Pins" slope		100	1009	423	26	4	5	0	0	1
Northern seamounts	Antigonia	180	577	344	18	6	15	5	4	3
	Munida	86	590	357	11	4	10	5	3	3
	Jumeau Ouest	234	810	357	18	4	15	4	4	3
	Crypthelia	185	1190	394	20	2	15	1	1	3
	Brachiopode	276	762	401	14	2	12	2	4	4
	Stylaster	420	923	502	17	2	8	1	2	4
	Jumeau est	377	1434	538	25	4	9	1	3	4
	Refractaire	640	820	707	9	0	2	0	1	1
Southern seamounts	Kaimon Maru	227	896	335	19	2	18	2	5	2
	Eponge	500	1144	612	18	6	13	3	2	4
	Introuvable	555	1040	639	17	4	9	3	1	5
	Zorro	609	1100	762	8	2	5	0	0	1
	Trois mousquetaires	609	1150	804	9	3	3	0	0	2
Total number of species sampled on the two Norfolk cruises						11	36	8	9	5
Total number of species known in the Southwest Pacific						24	79	21	27	14

Minimum, maximum and mean depth and number of sampled stations are indicated for each seamount during the NORFOLK1 and NORFOLK2 campaigns. The first line includes the results from the stations sampled on the "Isle des Pins" slope. The eight following lines correspond to the northern seamounts ordered by mean depth and the next five lines correspond to the southern seamounts and are also ordered by mean depth. For each genus the total number of species sampled over the "Isle des Pins" slope and each seamount is indicated

Table 2 List of species of Galatheidae and *Eumunida* (Chirostylidae) identified in the samples from the NORFOLK1 and NORFOLK2 campaigns and their occurrences in samples from other campaigns of the Tropical Deep-Sea Benthos program (http://www.mnhn.fr/musorstom) represented in the MNHN collections

Species	Results from sampling of the Norfolk 1 and Norfolk 2 cruises															Results from all other cruises of the tropical deep sea benthos program											
	Brachiopode	Stylaster	Jumeau Ouest	Jumeau Est	Introuvable	Trois Mousquetaire	Zorro	Eponge	Kaimon Maru	Réfractaire	Antigonia	Cryphelia	Munida	Isle des Pins slope		N. Caledonia slope	Chesterfield Is.	Loyalty Is.	Vanuatu	Matthew & Hunter	Wallis & Futuna	Indonesia	N.E. Australia	Polynesia	Fidji	Philippines	Depth range (m)
Agononida alisae	0	0	0	0	0	0	0	0	0	0	1	0	0	0		0	0	0	1	0	0	0	0	0	0	0	385-440
Agononida collirrhoe	0	0	0	0	0	0	0	1	0	0	1	0	1	0		1	1	1	0	0	0	0	0	0	1	0	241-575
Agononida eminens	0	0	0	0	0	0	1	0	0	0	0	0	0	0		1	1	0	1	0	1	1	1	0	1	0	564-1000
Agononida incerta	0	0	0	0	0	0	0	0	0	0	1	0	1	1		1	1	1	1	1	0	1	1	0	1	1	17-720
Agononida insolita & aff. insolita	0	0	1	0	0	0	0	0	0	0	1	0	0	0		1	0	0	0	0	0	0	0	0	1	0	260-950
Agononida laurentae	0	1	1	1	0	1	0	1	0	0	1	1	1	1		1	1	1	1	1	0	0	0	0	1	0	260-573
Agononida marini	0	0	0	1	1	1	0	1	0	0	0	0	0	0		1	1	1	0	0	0	0	0	0	0	0	463-600
Agononida normani	0	0	0	0	1	0	0	0	0	0	0	0	0	0		1	0	0	1	0	1	0	0	0	1	0	320-668
Agononida ocyrhoe	1	1	1	1	1	0	0	1	1	0	0	0	0	1		1	1	0	1	0	1	0	0	0	1	0	420-650
Agononida procera	0	0	0	0	1	1	1	1	0	0	0	0	0	0		1	0	0	0	0	0	0	1	0	1	0	680-750
Agononida sphecia	1	0	1	1	0	0	0	1	1	0	1	1	1	1		1	1	1	0	0	0	0	0	0	1	0	59-520
total number of *Agononida sp.*	2	2	4	4	4	3	2	6	2	0	6	2	4	4		10	7	5	6	2	3	2	3	0	9	1	
Eumunida aff keijii	0	0	0	0	1	0	0	0	0	0	0	0	0	0		0	1	0	0	0	0	0	0	0	0	0	470-950
Eumunida annulosa	1	1	1	1	1	1	1	1	1	0	1	1	1	1		1	1	0	0	0	0	0	0	0	0	0	375-650
Eumunida capillata	1	1	1	1	1	0	0	1	0	0	1	0	1	0		1	1	0	0	0	0	1	0	0	0	0	356-600
Eumunida parva	1	1	1	1	1	1	0	1	1	1	0	1	1	0		1	0	0	0	0	0	0	0	0	0	0	428-545
Eumunida sternomaculata	1	1	0	1	1	0	0	1	0	0	1	1	0	0		1	0	0	0	0	0	0	0	0	0	0	418-650
total number of *Eumunida sp.*	4	4	3	4	5	2	1	4	2	1	3	3	3	1		4	3	0	0	0	0	1	0	0	0	0	
Munida acantha	1	0	1	1	0	0	0	0	1	0	1	1	1	0		1	0	1	0	0	0	0	0	0	0	0	59-460
Munida alonsoi	1	1	1	0	1	0	0	1	0	0	0	0	0	0		1	1	0	0	0	0	0	0	0	0	0	448-680
Munida amblythes	0	0	0	0	0	0	1	0	0	0	0	0	0	0		1	0	0	0	0	0	0	0	0	1	0	525-1000
Munida armilla	0	0	1	0	1	0	0	1	1	0	0	0	0	0		1	0	0	0	1	1	0	0	0	1	0	233-700
Munida barangei	1	0	0	0	0	0	0	0	0	0	0	0	0	0		1	0	0	0	0	0	0	0	0	0	0	410-500
Munida callista	1	0	1	1	0	0	0	1	1	0	0	1	0	0		1	1	0	0	0	1	0	0	0	1	0	327-590
Munida elinata	0	0	0	0	0	0	0	0	1	0	0	1	1	0		1	1	0	1	0	1	1	0	0	1	1	28-245
Munida congesta	0	0	0	0	0	1	1	1	0	1	1	0	1	0		1	0	0	1	0	0	0	0	0	1	0	536-787
Munida distiza	0	0	1	0	0	0	0	0	0	1	0	1	0	0		1	1	0	0	0	0	0	0	0	0	0	400-590
Munida eclepsis	1	1	1	1	1	1	1	1	1	0	1	1	1	0		1	0	0	0	0	0	0	0	0	1	0	400-600
Munida gordoae	0	0	0	0	0	0	0	0	1	0	0	1	0	0		1	1	1	1	1	0	0	0	0	1	0	80-307
Munida guttata	0	0	1	0	0	0	0	0	1	0	1	1	0	0		1	0	1	0	0	1	0	0	0	1	0	170-320
Munida hyalina	0	0	0	0	0	0	0	0	0	0	0	1	0	0		1	1	0	0	0	0	1	0	0	1	0	205-720
Munida leagora	1	1	1	1	0	0	0	1	1	0	1	1	1	0		1	1	0	1	0	1	0	0	0	1	0	240-580
Munida moliae	0	0	0	1	0	0	0	0	1	0	0	1	0	0		1	0	1	0	0	1	0	0	0	1	0	263-575
Munida notata	0	0	0	0	0	0	0	1	1	0	1	0	1	1		1	1	1	1	0	1	0	0	0	1	0	120-850
Munida ommata	1	0	1	1	0	0	0	0	1	0	0	1	1	0		1	1	1	0	0	0	0	0	0	1	0	205-610
Munida parile	0	0	0	0	1	0	0	0	0	0	0	0	0	0		1	0	0	0	0	0	0	0	0	0	0	562-616
Munida pectinata	0	0	0	0	0	0	0	0	1	0	0	1	0	0		1	0	0	0	0	0	0	0	0	0	0	562-616
Munida psamathe	0	1	0	0	1	1	1	1	0	0	0	0	0	0		1	0	0	0	1	1	0	0	0	0	0	500-700
Munida psylla	0	0	1	1	0	0	0	1	0	0	0	0	0	0		1	0	1	0	0	0	0	0	0	0	0	380-573
Munida pygmaea	0	0	0	0	1	0	0	0	0	1	0	0	0	0		1	0	0	0	0	0	0	0	0	1	0	220-824
Munida rhodonia	0	0	0	0	0	0	0	0	0	0	1	0	0	0		1	1	1	1	0	0	0	0	0	1	0	395-753
Munida rostula	0	0	0	0	0	0	1	0	0	0	0	0	0	0		1	1	1	0	0	1	0	0	0	1	0	465-880
Munida rubrodigitalis	0	1	1	0	1	0	0	1	1	0	1	0	0	0		1	0	1	1	0	0	0	1	0	0	0	425-650
Munida rufiantennulata	1	0	1	0	0	0	0	1	1	0	0	0	0	0		1	1	1	1	1	0	1	0	0	1	1	167-705
Munida runcinata	0	0	0	0	0	0	0	0	0	0	1	0	1	0		1	0	1	1	0	1	0	0	0	1	0	245-509
Munida simulatrix	0	0	0	0	0	0	0	0	1	0	1	0	0	0		1	0	1	0	0	0	0	0	0	0	0	335-443
Munida spilota	0	0	0	0	0	0	0	0	0	0	1	0	0	0		1	0	0	0	1	0	0	0	0	0	0	220-400
Munida stia	1	1	0	0	0	0	0	0	0	0	0	0	0	0		1	1	0	0	0	0	0	0	0	0	0	360-610
Munida stigmatica	0	0	0	0	0	0	0	0	1	0	0	1	0	0		1	1	0	0	1	0	0	0	0	0	0	233-400
Munida taenia	1	0	1	0	0	0	0	0	0	0	1	1	0	1		1	1	0	0	0	0	0	0	0	0	0	200-400
Munida thoe	1	1	1	1	1	0	0	1	1	0	1	1	1	1		1	0	0	0	1	1	0	0	0	0	0	220-430
Munida thyche	0	0	0	0	0	0	0	0	0	0	0	0	0	1		1	1	0	1	0	1	0	0	0	0	0	140-440
Munida tuberculata	0	0	0	0	1	0	0	0	0	0	0	0	0	0		1	0	0	1	1	1	0	0	0	1	0	285-608
Munida zebra	1	1	1	1	0	0	0	1	0	0	1	1	1	1		1	0	1	0	0	0	0	0	0	0	0	200-610
total number of *Munida sp.*	12	8	15	9	9	3	5	13	18	2	15	15	10	5		36	16	14	11	8	13	3	1	0	19	2	
Paramunida belone	0	0	0	0	0	0	0	0	0	0	1	0	1	0		1	0	1	0	0	1	0	0	0	1	0	245-487
Paramunida granulata	0	0	0	0	1	0	0	0	0	0	0	0	1	0		1	0	1	0	0	1	1	0	0	1	0	400-650
Paramunida labis	0	0	0	0	0	0	0	1	0	0	1	0	0	0		1	0	0	0	0	1	0	0	0	1	0	229-440
Paramunida luminata	0	0	1	0	1	0	0	0	0	0	0	0	0	0		1	0	0	0	0	1	0	0	0	0	0	400-440
Paramunida pictura	1	0	0	1	0	0	0	0	1	0	1	1	1	0		1	1	1	0	1	1	0	0	0	1	0	205-710
Paramunida pronoe	0	0	1	0	0	0	0	0	0	0	0	0	0	0		1	0	0	0	0	0	0	0	0	1	0	439-510
Paramunida stichas	0	1	1	0	1	0	0	1	0	0	1	0	1	0		1	0	0	0	1	1	0	1	1	1	1	210-590
Paramunida thalie	1	0	1	0	0	0	0	1	1	0	1	0	1	0		1	0	1	0	0	0	0	0	0	1	0	245-420
total number of *Paramunida sp.*	2	1	4	1	3	0	0	3	2	0	5	1	5	0		8	1	4	0	2	6	2	0	1	7	1	
Onconida alaini	0	0	1	0	0	0	0	0	0	0	1	0	0	0		1	1	1	0	0	0	0	0	0	0	0	200-575
Alainius crosnieri	1	1	0	1	0	0	0	1	0	1	0	0	1	0		1	0	1	0	0	0	0	0	0	0	0	90-600
Bathymunida nebulosa	0	0	1	0	0	0	0	0	1	0	0	0	0	0		1	1	0	0	1	0	0	0	0	0	0	300-610
Crosnierita dicata	0	0	0	0	0	0	0	0	0	0	1	0	0	0		1	0	1	1	0	0	0	0	0	1	0	281-440
Crosnierita urizae	1	0	1	1	0	0	0	0	0	1	0	1	1	0		1	1	0	0	1	0	0	0	0	0	0	230-610
Crosnierita yomte	1	0	0	0	0	0	0	0	1	0	1	0	0	0		1	0	0	0	0	0	0	0	1	1	0	95-487
Heteronida aspinirostris	1	1	1	1	1	0	0	1	1	0	0	0	0	0		1	1	1	1	0	0	0	0	0	0	0	345-930
Raymunida elegantissima	0	0	0	0	0	0	0	0	0	0	0	0	1	0		1	0	0	0	0	0	1	0	0	0	0	35-200
Phylladiorhynchus ikedai	0	0	0	0	0	0	0	0	1	0	0	0	0	0		1	0	1	0	0	0	1	0	0	0	0	200-210
total number of species from other Galatheidae genus	4	2	4	3	1	0	0	2	5	1	4	1	3	0		9	4	5	2	2	0	2	0	1	2	0	

Depth range of the stations where each species was sampled is indicated in the last column

seamounts. Except *Agononida alisae*, all Galatheidae species sampled from Norfolk seamounts during the two cruises were also known from the New Caledonia island slope (Table 2). However, only nine species were identified among specimens collected over the 26 stations explored on the slope Isle des Pins, although these stations covered a range of depth from 100 to 1,009 m. On average, we identified 17.8 species at 15.6 stations per seamount. When excluding the island slope, a significant correlation was found between the total number of species and the number of stations sampled per seamount ($r = 0.618$; $P = 0.024$). Thus, the number of species sampled per seamount is a reliable measure of the sampling effort. The diversity recovered for Chirostylidae (genus *Eumunida*) was comparable with that of Galatheidae, since we found 36% of the species known in the South Pacific over all the sampled seamounts (Tables 1, 2).

The total richness of the studied area was extrapolated to 70 species by Bootstrap estimator and 75 and 77 species, by the first- and second-order Jackknife estimators, respectively (Fig. 2). Thus, our sampling effort led to a sample of between 83 and 91% of the total Galatheidae estimated species diversity over this sampling area.

Genetic diversity

COI haplotypes were deposited at Genbank (Accession Nos. AY 800009-800046, AY 800048, AY 800050, AY 800051, AY 800055-800065, DQ 011181-011220). Genbank's entry for each haplotype included the geographic location of the specimens displaying this haplotype, the cruise during which each specimen was sampled, and the M.N.H.N. collection access number when available.

Except *M. acantha*, all species studied were polymorphic for the sequenced portion of the COI gene (Table 3). The variability was restricted to the first and third codon positions, where all substitutions were synonymous. No saturation was detected among any of the species studied at the first and the second codon position. A very weak saturation for the third position was detected only for the two *Eumunida* species: the slope of the linear regression (S) for the third codon position was, respectively, $S = 0.71$ for *E. annulosa* and $S = 0.73$ for *E. sternomaculata*. No saturation was observed for the *Munida* species and the gastropods.

Within Galatheidae, the two polymorphic *Munida* species differed by their levels and patterns of genetic diversity. The higher proportion of polymorphic sites, haplotype number, haplotypic and nucleotidic diversity was obtained in *M. thoe* (Table 3). The 29 haplotypes identified over the 35 *M. thoe* specimens were genetically close, as seen in the MSN (Fig. 3a). Specimens from the same seamounts were not obviously closer genetically than those from different seamounts.

Although six haplotypes were identified within the 36 *M. zebra* specimens analysed, 31 specimens collected on 10 different seamounts shared the same haplotype, leading to low haplotype diversity in this species. The five other haplotypes derived from this dominant haplotype (Fig. 3b), and only by one substitution. No geographic structure was observed.

Conversely, to those observed in *Munida* species, the slight differences in genetic diversity between the two *Eumunida* species could be attributed to sampling bias. Indeed, 23 haplotypes were detected for 34 specimens analysed in *E. annulosa* when 10 haplotypes were detected among the 20 specimens analysed for *E. sternomaculata* (Table 3). The MSN (Figs. 3c, 2d) shows that the sequenced gene was diversified within both species, but that there was not any obvious geographic structure.

The haplotype diversity was similar in the two gastropod species (Table 3). However, the nucleotide diversity of *N. problematica* was three times higher than that of *S. remensa*. The MSN showed two groups of distant haplotypes in the non-planktotrophic species (*N. problematica*, Fig. 3f), whereas all the haplotypes were closely related in the planktotrophic *S. remensa* (Fig. 3E). Moreover, the pattern was geographically structured in *N. problematica*, as all the individuals

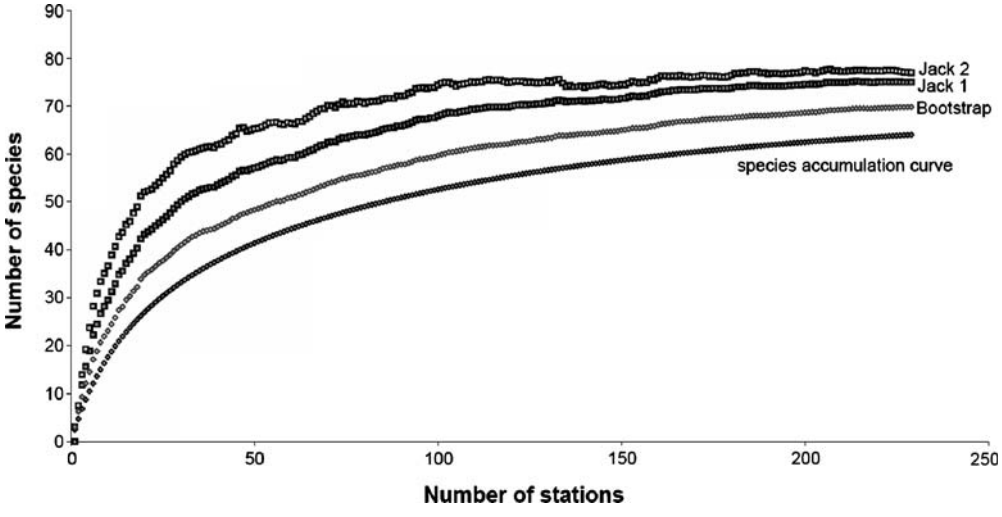

Fig. 2 Species accumulation curves based on EstimateS 7.5 (Colwell 2005); Jackknife (Jack 1, Jack 2) and Bootstrap richness estimators

Table 3 Sample size and summary statistics of the gene COI for each analysed species collected on Wallis and Futuna, "Isle des Pins" slope and Norfolk seamounts

Species	Wallis and Futuna	Isle des Pins	Northern area							Southern area			Sample size	Polymorphic sites	Haplotype number	Haplotype diversity (h)	Nucleotide diversity (π)
			AN	BR	CR	JE	JO	ST	MU	EP	IN	KM					
Munida thoe	1(1)	1	4(1)	2	3	4	4	3	2	4	4	3	35	5%	29	0.985	0.007
Munida zebra		4	4	5	4	4	4(1)	4	2	4		1(1)	36	1%	6	0.308	0.001
Munida acantha			8(8)	3	3	3			3			1(1)	21	0%	1	0	0
Eumunida annulosa		1	4	2	4	4	4	4	2	4	4	1	34	5%	23	0.963	0.009
Eumunida sternomaculata				4	1	4		5 (1)		3	3		20	2%	10	0.863	0.003
Sassia remensa		3	4		4	4	1		4			4	24	5%	21	0.986	0.009
Nassaria problematica		4			4	4				4	4	4	24	8%	14	0.946	0.021

The number of individuals analysed from previous campaigns are given in parentheses
AN Antigonia, *BR* Brachiopode, *CR* Crypthelia, *JE* Jumeau est, *JO* Jumeau ouest, *ST* Stylaster, *EP* Eponge, *IN* Introuvable, *KM* Kaimon-Maru

sampled on the island slope were genetically distant from those sampled on the seamounts. Furthermore, individuals sampled on the seamounts of the northern part of the ridge exhibited similar haplotypes, and those from the southern part of the ridge were also similar to one another. However, the genetic distances between haplotypes sampled on the seamounts, whether from the north or from the south, remained genetically closer to one another than the haplotypes from the island slope, which were genetically more distant from each other.

The trends observed in the MSN patterns were confirmed by AMOVA analyses (Table 4), which revealed no significant among-population contribution to the total sequence divergences in the galatheid species and in the planktotrophic gastropod *S. remensa*. Among-population variance components were not significantly different from zero, and we therefore were unable to reject the null hypothesis of absence of population structure. Conversely, for the non-planktotrophic gastropod *N. problematica*, the among-population variance component was highly significant ($P < 10^{-3}$). The null hypothesis could thus be rejected: the populations of *N. problematica* were genetically structured and the F_{ST} estimated to 0.814.

Likewise, the Mantel test (Table 5) failed to detect significant correlation between geographical and genetic distances in the galatheid species and in the planktotrophic gastropod *S. remensa*. Conversely, the correlation coefficient was positive and highly significant ($P < 10^{-3}$) in the non-planktotrophic gastropod *N. problematica*, where genetic distance was thus roughly in proportion to geographic distance.

Demographic history

The goodness-of-fit test to the model sudden expansion and the results of Tajima's *D* test performed on each species at the two sampling dates are given in Table 6. For all genetically not structured species, all histograms (data not shown) presented curves characteristic of populations with constant size over time. All species presented moderate to highly negative Tajima's *D* test values, although only one, *M. thoe* from the second cruise, was significant. The *E. sternomaculata* sample from the first cruise could not be fitted to an expansion model. For *N. problematica*, although the populations were markedly structured, due to small sampling size from each cruise, analyses were also conducted on sub-samples pooled by cruise (Table 6). Tajima's *D* test values were positive, although not significant. There was also no indication of population bottlenecks followed by expansion.

Discussion and conclusions

The two NORFOLK cruises allowed a comprehensive sampling of the species richness of the sampled area since 83–91% of the estimated total species richness of

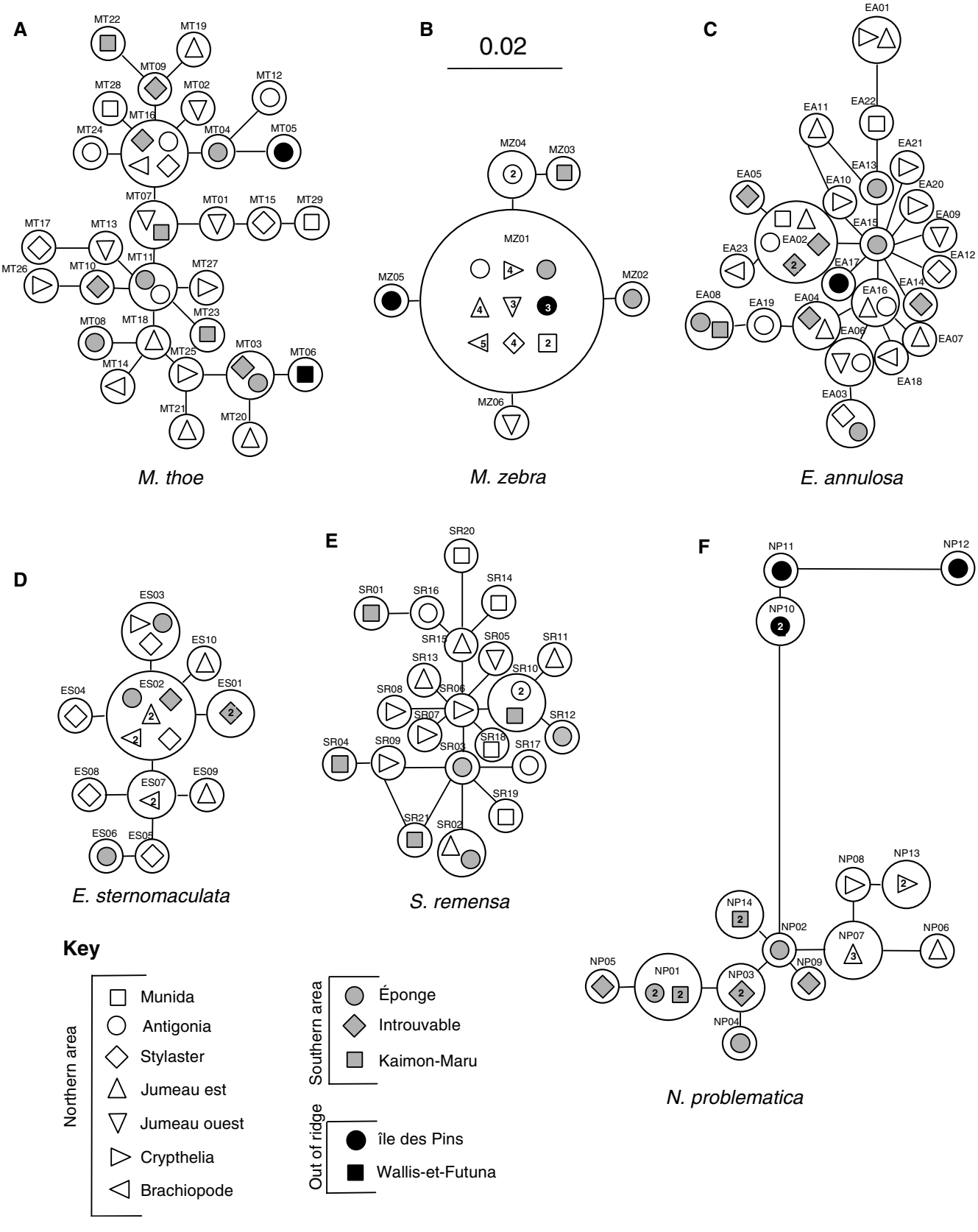

Fig. 3 Minimum spanning networks constructed using Tamura–Nei distances between mitochondrial COI haplotypes (represented by *circles*); areas proportional to the number of individuals sharing a given haplotype. The *symbols* inside the circle represent the localities where the haplotype was found (see key)

Table 4 Hierarchical partitioning of molecular variation within and among seamounts (AMOVA) based on COI haplotypes

Species	Source of variation	Degree of freedom	Variance component	F_{ST}	P value
Eumunida annulosa	Among populations	8	−0.091	NS	0.666
	Within populations	23	2.737		
Eumunida sternomaculata	Among populations	4	0.024	NS	0.304
	Within populations	14	0.857		
Munida thoe	Among populations	9	0.038	NS	0.309
	Within populations	23	1.917		
Munida zebra	Among populations	8	0.017	NS	0.056
	Within populations	25	0.131		
Sassia remensa	Among populations	5	−0.084	NS	0.745
	Within populations	17	2.521		
Nassaria problematica	Among populations	5	5.770	0.811	$< 10^{-3}$
	Within populations	18	1.345		

P value: Probability of obtaining by chance equal or more extreme random variance component and F_{ST} than the observed values

Galatheidae (excluding genera *Galathea* and *Munidopsis*) was sampled. However, each individual seamount appeared to be richer than the restricted explored area on the New Caledonia slope, although a similar area to that of one seamount was sampled. Indeed, over each seamount an average of more than one species was added per station explored and a positive correlation between the number of stations explored and the number of species sampled indicates that not all the species living on each seamount were sampled despite the high sampling effort. In the two NORFOLK cruises, the number of species added per sampled station from the New Caledonian slope was about three times lower even though sampling effort was similar to that made on each seamount explored. It is therefore likely that, for any given restricted area, species richness is lower along the "continental" slope than in each explored seamount along the Norfolk ridge (i.e. species density is lower in the former).

The observed Galatheoidea group species richness is remarkably high on the Norfolk ridge seamounts and the Isle des Pins slope since it represents 42% of the known diversity of the South Pacific for Galatheidea and 36% for the genus *Eumunida*. The species of the families Galatheidae and Chirostylidae are among the best-inventoried marine taxa in New Caledonia. All Museum collections obtained from more than 28 cruises, covering more than 1,500 stations during the last 20 years, have been thoroughly studied (de Saint Laurent and Macpherson 1990; Macpherson 1993, 1994; Baba and de Saint Laurent 1996; Machordom and Macpherson 2004; Macpherson and Machordom 2005; Baba 2004, 2005 and K. Baba personal communication) and have allowed the description of more than 150 new species for the Galatheoidea group. This remarkable inventory reveals that species diversity is particularly high in these families. Nevertheless, despite the high diversity found on the Norfolk seamounts, none of the species sampled was found to be endemic either to one seamount or even to the entire ridge. Indeed, all the sampled species were known from the island slope of New Caledonia, indicating that the Norfolk seamounts are a diversity hotspot for the family Galatheidae, 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 seamounts are not an area of high endemism, they are highly productive zones where many species co-occur in large populations. This finding is in accordance with the suggestion that high productivity is a prominent ecological feature of seamounts (Fock et al. 2002; Genin 2004; Rogers 1994). The high productivity observed on seamounts could either result from enhanced primary production or be due to the fact that seamounts offer a location where the deep scattering layers can intersect hard substrate.

Table 5 Mantel correlation test between genetic distances (Tamura–Nei) matrix based on COI haplotypes and geographical distances matrix between individuals

Species	Correlation coefficient	P value
Eumunida annulosa	0.000	0.89
Eumunida sternomaculata	−0.007	0.49
Munida thoe	0.040	0.41
Munida zebra	0.155	0.12
Sassia remensa	0.249	0.05
Nassaria problematica	0.701	$< 10^{-3}$

P value: Probability of obtaining by chance equal or more extreme random correlation coefficient than the observed value

The analysis of population genetic structure in species of Galatheidae and Chirostylidae suggested that their populations are genetically connected between the explored seamounts. Except for *M. acantha*, the within-species diversities of the studied fragment of COI gene were important but no genetic structure among populations was observed in most species. However, with the same gene and with a lower level of haplotypic and nucleotide diversity, Fratini and Vannini (2002) revealed that geographically close populations of the swimming

Table 6 Neutrality test and test of goodness of fit to the model sudden expansion, for each species and each sampling date

	Eumunida annulosa		*Eunmunida sternomaculata*		*Munida zebra*		*Munida thoe*		*Sassia remensa*		*Nassaria problematica*	
	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2	N1	N2
Neutrality tests												
Tajima's *D*	−0.62	−0.97	−0.54	−0.97	−1.29	−1.11	−1.16	−1.65	−1.06	−1.10	0.14	1.21
P value	0.29	0.19	0.32	0.19	0.10	0.15	0.13	**0.04**	0.16	0.16	-0.44	−0.14
Test of goodness-of-fit												
Sum of squared deviation	0.03	0.01	No fit	0.90	0.00	0.00	0.01	0.00	0.01	0.05	0.04	0.12
P (Sim. Ssd > = Obs. Ssd)	0.05	0.64		0.17	0.29	0.33	0.58	0.41	0.23	0.26	0.24	0.05

The two sampling dates correspond to the two cruises NORFOLK1 (N1) and NORFOLK2 (N2)
In bold, significant *P* values

crab *Scylla serrata*, which has an extended planktonic larval phase, were differentiated. Thus, the absence of genetic structure appears not to be a consequence of a lack of variability for the marker used. The saturation analysis confirmed that genetic homogeneity among seamounts was also not due to homoplasy. Moreover, the variability of the marker is likely to be neutral since all the mutations identified were found to be synonymous. Similarity between haplotypes is thus due to community of descent and, since no selective pressure may be inferred from the observed variability, the absence of genetic structure can be interpreted to result from gene flow among populations. However, this pattern of genetic structure may also be found in recently isolated population that have not experienced complete lineage sorting. Moreover, if isolation was not associated with a population bottleneck (e.g. an important reduction of effective size) the time before complete lineage sorting may be long. However, the high variability of reproductive success in many marine organisms should lead to reduced effective population size (Flowers et al. 2002; Hedgecock 1994; Turner et al. 1999) and thus rapid lineage sorting when two populations are isolated. Moreover, seamounts are not ephemeral structures (typically millions to tens of millions of years in age). Thus, if hydrological phenomena efficiently prevent gene flow among close seamounts over time, the lineage sorting should be observed in most populations. Lastly, for each species, at sampling scale of each cruise, Tajima *D* test revealed no departure from mutation-drift equilibrium and the mismatch analysis of pairwise differences were characteristic of populations with constant size over time.

In *M. thoe*, the haplotype of the specimen collected from Wallis and Futuna, ca. 2,200 km distant, was genetically very close to those of specimens sampled from the Norfolk seamounts. This observation suggests that the dispersal abilities of this species allow large-scale gene flow among populations, or recent connection between the populations. Our results parallel those obtained by Smith et al. (2004) from deep-sea bamboo corals, among which taxonomists had traditionally suggested a high rate of endemism on seamounts and low gene flow among distant populations. Their genetic survey confirmed that specific diversity is high, but showed that species are not endemic to seamounts and that distant populations are genetically interconnected. This pattern may therefore be a general phenomenon.

Two gastropod species were used to differentiate between the effects of their life cycles and those of physical fragmentation of populations resulting from hydrological phenomena. In gastropod the morphology of the protoconch allows inference of the type of larval development, which is itself related to dispersal ability. This relation has been confirmed by many studies of population genetic structure that, comparing close species contrasting in the duration of pelagic larval development, have shown that species with poorly dispersive larvae are highly structured, whereas those with highly dispersive larvae are poorly structured (Boisselier-Dubayle and Gofas 1999; Collin 2001; Kyle and Boulding 2000; Todd et al. 1998). Our data confirm this trend by showing that the non-planktotrophic species in our species sample, *N. problematica*, is highly structured. By contrast, like the galatheid species, in the planktotrophic *S. remensa* no genetic structure was revealed by our study. An alternative hypothesis is that the two species differ by their population effective size. Following this hypothesis, the absence of genetic differentiation within *S. remensa* is not subsequent to gene flow among seamounts but may be due to a very high effective population size that has not yet permitted lineage sorting. Last, given the very high F_{ST} value estimated among populations of *N. problematica*, it might be possible that the observed population structure is not due to a high limitation of gene flow within species but to the presence of cryptic species. The MSN revealed that the specimens from the New Caledonia slope are genetically highly distant from the specimens found on the seamounts. The MSN also revealed that, although the seamount populations are differentiated, the genetic distances between haplotypes are weak. It is thus possible that the species present on the New Caledonia slope differs from that sampled on seamounts.

Other studies on Atlantic seamounts revealed the same trends. Indeed, in the North Atlantic, Gofas (2000), examining Fasciolariidae 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 both for galatheid species and for planktotrophic and non-planktotrophic gastropod species suggest that seamounts are not particularly isolated patches of habitat. Moreover, when comparing molluscan fauna from North Atlantic and Azores seamounts to the mainland, planktotrophic development appears over-represented (Gofas and Beu 2002). The trends observed on the distribution of molluscs on North Atlantic seamounts are similar to those we observed for squat-lobster in Norfolk ridge seamounts; there is no limitation of dispersal and seamounts do not represent isolated patches of habitat.

Overall, these results strongly suggest that the hydrological phenomena that may be associated with seamounts are not strong physical barriers for the species inhabiting them. The endemism associated with oceanic islands is traditionally explained by the acceleration of evolutionary processes in isolated populations (Barton 1998) in which small population size and lack of genetic exchange with larger gene pools induce rapid genetic drift. Moreover, local adaptation, resulting from local selection, is thought to be facilitated by genetic isolation as migration does not bring misadapted genotypes. Our data suggest that, contrary to this insular isolation model, populations living on seamounts appear to be genetically connected, and the high diversity observed on seamounts therefore may not result from high local speciation rate. Both species distribution patterns within Galatheidae and the genetic structure within several species sampled on nine seamounts of the Norfolk ridge indicate that, rather than representing areas of endemism, these areas should be regarded as highly productive zones that may accommodate many species in densities far higher than in surrounding less-productive areas. Thus, our data fit best with the oases model.

Seamounts are of great interest for biodiversity conservation because widespread species concentrate in large numbers and in dense populations within these small areas. Contrary to previously held belief, however, these intriguing areas are not characterized by distinctive faunas that do not occur elsewhere. Protecting seamount area would thus preserve particularly rich communities and ecosystems (Roberts 2002). Moreover, their preservation would protect number of species in a minimal area that are easier to control. Ecosystems, at least as much as individual species, if not more, justify protection because they constitute the level at which survival of individual species is sustainable. Apparent lack of endemism (or at least its low level) in seamounts does not diminish their potential as biodiversity reserves, but rather changes the perspective in which such reserves should be created. However, as exemplified by *N. problematica* in our study, some species of invertebrates inhabiting seamounts have a low dispersal capacity (Parker and Tunniclife 1994); in order to develop a better global understanding of seamount habitats, a special effort will have to be done to describe the reproductive strategy of additional deep-sea invertebrate groups.

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References

Aboim MA (2005) Population genetics and evolutionary history of some deep-sea demersal fishes from the Azores - North Atlantic. University of Southampton, Faculty of Enginering Science and Mathematics, School of Ocean and Earth Science, PhD Thesis, 167 pp

Aboim MA, Menezes GM, Schlitt T, Rogers AD (2005) Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. Mol Ecol 14:1343–1354

Baba K (2004) *Uroptychodes*, new genus of Chirostylidae (Crustacea: Decapoda: Anomura), with description of three new species. Sci Mar 68:97–116

Baba K (2005) Deep-sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-Pacific, with a list of species. Galathea Rep 20:1–317

Baba K, Saint-Laurent M de (1996) Crustacea Decapoda: rev on of the genus *Bathymunida* Balss, 1914, and description of six new related genera (Galatheidae). Mém Mus Nat Hist Nat 168:433–502

Barton NH (1998) Natural selection and random genetic drift as causes of evolution on islands. In: Grant PR (ed) Evolution on islands. Oxford University Press, Oxford, pp 102–123

Boehlert GW, Mundy BC (1993) Ichtyoplancton assemblages at seamounts and oceanic islands. Bull Mar Sci 53:336–361

Boisselier-Dubayle MC, Gofas S (1999) Genetic relationships between marine and marginal-marine populations of Cerithium species from the Mediterranean Sea. Mar Biol 135:671–682

Collin R (2001) The effects of mode of development on phylogeography and population structure of North Atlantic *Crepidula* (Gastropoda: Calyptraeidae). Mol Ecol 10:2249–2262

Colwell RK (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at: http://www.purl.oclc.org/estimates

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Phil Trans Roy Soc (B) 345:101–118

Creasey S, Rogers AD (1999) Population genetics of bathyal and abyssal organisms. Adv Mar Biol 35:3–151

Dijkstra HH, Gofas S (2004) Pectinoidea (Bivalvia: Propeamussiidae and Pectinidae) from some northeastern Atlantic seamounts. Sarsia 89(1):33–78

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491

Flowers JM, Schroeter SC, Burton RS (2002) The recruitment sweepstakes has many winners: genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. Evolution 56:1445–1453

Fock H, Uiblein F, Koester F, von Westernhagen H (2002) Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. Mar Biol 141:185–199

Folmer O, Black M, Hoen W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 3:294–299

Fratini S, Vannini M (2002) Genetic differentiation in the mud crab *Scylla serrata* (Decapoda: Portunidae) within the Indian Ocean. J Exp Mar Biol Ecol 272:103–116
Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J Mar Syst 50:3–20
Gofas S (2000) Four species of the family Fasciolariidae (Gastropoda) from the North Atlantic seamounts. J Conchol 37:7–16
Gofas S, Beu A (2002) Tonnoidean gastropods of the North Atlantic seamounts and the Azores. Amer Malacol Bull 17:91–108
Hassanin A, Lecointre G, Tillier S (1998) The 'evolutionary signal' of homoplasy in protein-coding gene sequences and its consequences for a priori weighting in phylogeny. Evolution 321:611–620
Hedgecock D (1994) Does variance in reproductive success limit effective population sizes of marine organisms? In: Beaumont AR (ed) Genetics and evolution of aquatic organisms. Chapman and Hall, London, pp 122–134
Heinz P, Ruepp D, Hemleben C (2004) Benthic foraminifera assemblages at Great Meteor Seamount. Mar Biol 144:985–998
Koslow JA, Gowlett-Holmes K, Lowry J, O'Hara T, Poore G, Williams A (2001) The seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar Ecol Progr Ser 213:111–125
Kyle CJ, Boulding EG (2000) Comparative population genetic structure of marine gastropods (*Littorina* spp.) with and without pelagic larval dispersal. Mar Biol 137:835–845
Machordom A, Macpherson E (2004) Rapid radiation and cryptic speciation in galatheid crabs of the genus Munida and related genera in the South West Pacific: molecular and morphological evidence. Mol Phyl Evol 33:259–279
Macpherson E (1993) Crustacea Decapoda: Species of the genus *Paramunida* Baba, 1988 (Galatheidae) from the Philippines, Indonesia and New Caledonia. Mém Mus Nat Hist Nat 156:443–473
Macpherson E (1994) Crustacea Decapoda: Studies on the genus *Munida* Leach, 1820 (Galatheidae) in New Caledonian and adjacent waters with descriptions of 56 new species. Mém Mus Nat Hist Nat 161:421–569
Macpherson E, 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. J Nat Hist 39:819–834
Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220
Miyazaki JI, Shintaku M, Kyuno A, Fujiwara Y, Hashinoto J, Iwasaki H (2004) Phylogenetic relationships of deep-sea mussels of the genus *Bathymodiolus* (Bivalvia: Mythilidae). Mar Biol 144:527–535
Morrison CL, Harvey AW, Lavery S, Tieu K, Huang Y, Cunningham CW (2002) Mitochondrial gene rearrangement confirm the parallel evolution of the crab-like form. Proc R Soc London B Biol Sci 269:345–350
Mullineaux LS, Mills SW (1996) A test of the larval retention hypothesis in semount-generated flows. Deep Sea Res I 44:745–770
Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York
Parker T, Tunnicliffe V (1994) Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. Biol Bull 187:336–345
Richer de Forges B, Koslow JA, Poore GC (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405:944–947
Richer de Forges B, Chauvin C (2005) Indo-Pacific deep-sea fauna: species richness and vulnerability of seamount fauna. Assises de la Recherche Française dans le Pacifique 24–27 Août 2004, 37–38 (Abstract)
Roberts CM (2002) Deep impact: the rising toll of fishing in the deep sea. TREE 17:242–245
Roden GI (1987) Effects of seamounts and seamount chains on oceanic circulation and thermocline structure. In: Keating BH et al. (eds) Seamounts, islands and atolls, Geophysical Monographs Ser 43. AGU, Washington DC pp 335–354
Rogers AD (1994) The biology of seamounts. Adv Mar Biol 30:305–350
Saint Laurent M de, Macpherson E (1990) Crustacea Decapoda: Le genre *Eumunida* (Chirostylidae) dans les eaux néo-calédoniennes. Mém Mus Nat Hist Nat 145:227–288
Sanger F, Nicklen S, Coulson AR (1977) DNA sequencing with chain-terminating inhibitors. Proc Natl Acad Sci USA 74:5463–5467
Schneider S, Dueffer JM, Roessli D, Excoffier L (2000) Arlequin ver 2.0: A software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland. URL: http://www.anthropologie.unige.ch/arlequin
Smith PJ, McVeagh SM, Mingoia JT, France SC (2004) Mitochondrial DNA sequence variation in deep-sea bamboo coral (Keratoisidinae) species in the southwest and northwest Pacific Ocean. Mar Biol 144:253–261
Swofford DL (1993) PAUP: phylogenetic analysis using parsimony. Illinois Natural History Survey, Champaign
Tajima F (1983) Evolutionary relationship of DNA sequences in finite populations. Genetics 105:437–460
Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595
Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol Biol Evol 10:512–526
Todd CD, Lambert WJ, Thorpe JP (1998) The genetic structure of intertidal populations of two species of nudibranch molluscs with planktotrophic and pelagic lecithotrophic larval stages: are pelagic larvae "for" dispersal? J Exp Mar Biol Ecol 228:1–28
Turner TF, Richardson LR, Gold JR (1999) Temporal genetic variation of mtDNA and effective female population size of red drum in the northern Gulf of Mexico. Mol Ecol 8:1223–1230
Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370
Won Y, Hallan SJ, O'Mullan GD, Vrijenhoek RC (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiolus*) from eastern Pacific hydrothermal vents. Mol Ecol 12:3185–3190
Worm B, Lotze HK, Myers RA (2003) Predators diversity hotspots in the blue ocean. Proc Natl Acad Sci USA 100:9884–9888