

Long-term monitoring of coastal benthic habitats in the Kerguelen Islands: a legacy of decades of marine biology research

J.-P. Féral¹✉, E. Poulin², C.A. González-Wevar³, N. Améziane⁴, C. Guillaumot⁵,
E. Develay⁵ and T. Saucède⁵

¹ Aix Marseille Université/CNRS/IRD/UAPV, IMBE-Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale, UMR 7263, Station Marine d'Endoume, Chemin de la Batterie des Lions, 13007 Marseille, France

² LEM-Laboratorio de Ecología Molecular, Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, CP 7800003, Ñuñoa, Santiago, Chile

³ CENTRO FONDAP IDEAL, Instituto de Ciencias Marinas y Limnológicas (ICML), Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile

⁴ MNHN/CNRS/UPMC/EPHE, ISYEB – Institut de Systématique Evolution Biodiversité, Station de Biologie Marine, BP 225, 29182 Concarneau Cedex, France

⁵ Université Bourgogne Franche-Comté, CNRS, Biogéosciences, UMR 6282, 6 boulevard Gabriel, 21000 Dijon, France

✉ Corresponding author: jean-pierre.feral@imbe.fr

Abstract

In the current context of climate change, sea-surface temperature variation, sea level rise and latitudinal shifts of currents and hydrological fronts are expected to affect marine biodiversity of the sub-Antarctic Islands, particularly in coastal waters. Characterising the impacts of climate change on marine communities requires recording environmental modifications through the establishment of long-term monitoring. PROTEKER aims at the establishment of a submarine observatory consisting of multi-disciplinary research: oceanography, habitat mapping and species inventories, genetic, eco-physiological and trophic analyses. It also aims to provide scientific standards for the management of the Kerguelen Marine Reserve. Eighteen sampling sites of previous programs were revisited by scuba diving among which eight were selected for monitoring and were progressively equipped. ROV observations and beam trawling have also been conducted for contextualisation. These sites (Morbihan Bay (4), North (2) and South (2) coast) are monitored using photo/video surveys, temperature and salinity sensors, and settlement plots. Sessile communities collected on settlement plots will be characterised yearly through morphological and DNA techniques. Phylogeographical studies of target taxa are being conducted to improve our knowledge of endemism and connectivity levels among sub-Antarctic islands.

Suivi à long terme des habitats benthiques côtiers des îles Kerguelen : l'héritage de décennies de recherche en biologie marine

Résumé

Dans le contexte actuel du changement climatique, le réchauffement des eaux marines de surface, l'élévation du niveau de la mer ainsi que les déplacements latitudinaux des courants et des fronts hydrologiques risquent d'affecter la biodiversité marine des îles subantarctiques, en particulier en zone côtière. Pour caractériser l'impact des changements climatiques sur les communautés marines il est nécessaire d'enregistrer en continu les modifications environnementales à travers un suivi sur le long terme. Dans ce but, le programme de recherche pluridisciplinaire PROTEKER a été mis en place pour constituer

un observatoire sous-marin des effets du changement climatique sur les habitats benthiques côtiers des Îles Kerguelen en couplant des approches complémentaires : océanographie, cartographie d'habitats et inventaires d'espèces, analyses génétiques, écophysiologiques et trophiques. Il vise également à fournir des critères scientifiques pour la gestion de la réserve marine des Kerguelen. Dix-huit sites d'échantillonnage ont été revisités en plongée sous-marine parmi lesquels huit ont été sélectionnés pour le suivi. Ils ont été progressivement équipés, puis des observations en ROV et des chalutages ont également été effectués afin de mieux connaître le contexte environnemental de chaque site. Les suivis (baie du Morbihan (4), côte nord (2) et côte sud (2)) sont réalisés à l'aide de relevés photo / vidéo, de capteurs de température et de salinité, et de placettes de colonisation. Les communautés sessiles collectées sur les placettes seront caractérisées chaque année par des approches morphologiques et moléculaires. Des études phylogéographiques sur des taxons cibles sont en cours afin d'améliorer notre connaissance des niveaux d'endémisme et de connectivité entre les îles subantarctiques.

Keywords: sub-Antarctic islands, climate change, frontal shifts, marine reserve, benthos monitoring, thermo recorders, settlement plots, artificial reefs, habitat mapping, scientific diving

Introduction

Historical background

Marine biology research on the Kerguelen Plateau has a long history, starting with the expedition of HMS *Challenger* (7 December 1873 to 31 January 1874), supported later by the establishment of a permanent scientific base (1951) and consolidated by intensive work during the cruises of the RV *Marion Dufresne* in the 1970s and 1980s. These studies have been extensively reviewed and summarised by Hureau (2011) while research specifically on benthic fauna was reviewed by Améziane et al. (2011). However, relatively few studies were dedicated to benthic invertebrates, and to benthic communities of coastal areas in particular (Grua, 1964a, 1964b, 1971, 1973, 1974; Arnaud, 1974). In addition to remoteness and often harsh conditions at sea, the lack of maritime means (vessel and/or funding) engaged for scientific work was one of the main factors limiting the advance of coastal benthic studies. From 1970 to 1989, the FV *La Japonaise*, an old converted 14 m long whaling boat moored at Port-aux-Français, was used for short coastal research programs. However, she was unfit to sail at sea, outside Baie du Morbihan, and could not access remote areas of the northern and southern Kerguelen coasts. From 1990 to 2003, the permanent presence of the RV *La Curieuse*, a 24 m long trawler, made it possible to work all around the main island and to implement more comprehensive programs, including the exploration of several sites along the northern and southern coasts of the main island (Féral and Poulin, 2011), the western coast having almost never been explored nor investigated

due to harsh sea conditions. Since 2011, the RV *La Curieuse* has sailed in the Kerguelen Islands during the austral summers, permitting the setting up and the implementation of a submarine coastal observatory of benthic life (Féral et al., 2016).

First investigations of macrobenthos of the Kerguelen Islands were based upon samples collected from soft-bottom substrates by means of dredges and grabs (Desbryères and Guille, 1973; Arnaud, 1974; Guille, 1977). These gears cannot be used for studies of hard-substrate communities, which are very common in the Kerguelen near-shore areas. In contrast, scuba diving proved to be a convenient approach to observe, explore, survey and experiment in shallow waters but it was scarcely used in the past. Scientific diving (SD) in Antarctic and sub-Antarctic open waters began to be used during the late 1940s and 1950s. In the Southern French Territories, P. Grua made scuba dives at Saint-Paul and (New) Amsterdam Islands in the 1958/59 season (Grua, 1963). Together with A. Tanguy, he made scuba dives at Crozet Islands (Possession Island on 17 and 18 December 1962) and Kerguelen Islands, studying flora and fauna. These were pioneering SD on hard infralittoral substrates, located within the Baie du Morbihan, December 1962/February 1963 (Grua 1964a, 1964b). Only a decade later SD was used in the framework of the PhD thesis field work of J.-C. Duchêne (Duchêne, 1976). As in other countries, these first scientific dives also helped to improve our knowledge on human body acclimatisation to diving in cold waters (Grua, 1967). SD has systematically been applied to benthic studies since 1980. The presence of the RV *La*

Curieuse and the practise of SD have significantly increased our knowledge of the taxonomy (Grua, 1971, 1973, 1974), distribution (Poulin and Féral, 1995), and functional ecology (Guille and Lasserre, 1979; Féral, 1985; Féral and Magniez, 1985, 1988; Magniez, 1983; Magniez and Féral, 1988) of the coastal benthos. The access to most of the Kerguelen coastal areas for targeted sampling and underwater observations by SD allowed the achievement of original studies at the scale of the archipelago, presented in several PhD theses dealing with life cycle (Magniez, 1980; Mespoulhé, 1992), development biology (Schatt, 1985), origin of Antarctic biodiversity (Poulin, 1996; Poulin and Féral, 1996; Féral, 2002; Poulin et al., 2002) and phylogenetics and phylogeography (Gérard, 2008). These studies were achieved in the framework of the Benthos-Mac program (IFRTP/IPEV#195), which was devoted to physiological adaptations, evolutionary ecology and diversification processes. Former explorations of the Kerguelen coasts and scientific outputs of the last five decades of marine biology research in coastal areas proved invaluable when time had come to monitor the potential impact of climate change on the coastal benthos at representative sites.

Climate change at the sub-Antarctic islands

Marine ecosystems are globally undergoing rapid alterations due to direct anthropogenic disturbances (Doney et al., 2012) and from indirect, human-driven climate change (i.e. global warming). These alterations are expected to affect the functioning and the very subsistence of marine ecosystems (Hoegh-Guldberg and Bruno, 2010). Using mesocosms, Ullah et al. (2018) demonstrated that the combination (synergistic and antagonist) of water acidification and warming reduced energy flows between the different levels of trophic networks, from the first (primary producers and detritus) to the second (herbivores), and from the second to the third trophic level (carnivores). In addition, new species interactions can emerge in communities exposed to environmental changes (Albouy et al., 2014) and the structure of these trophic interactions is directly related to the potential resilience of ecosystems (Loreau and Behera, 1999; Hattab et al., 2016).

Sub-Antarctic islands are those islands of the Southern Ocean located north of, and adjacent to, the Antarctic Convergence or Polar Front (PF).

Recent observations indicate that this highly dynamic region is undergoing the direct and indirect consequences of climate change, as evidenced on land by glacier retreat, temperature increase, precipitation decrease, more frequent extreme events, increase in wind speed and annual rise of sunshine hours (Smith, 2002; Mélice et al., 2003; Rouault et al., 2005; Le Roux and McGeoch, 2008). It was proposed that climate change in the region was associated with the southward shift of the Antarctic Circumpolar Current (ACC) and in particular of its frontal systems, the sub-Antarctic Front (SAF) and the PF, which border sub-Antarctic islands (Allan et al., 2013). The ACC is a key oceanographic feature of the Southern Ocean and a major driver of marine ecosystem functioning (Tynan, 1998). The effects on marine environments include water chemistry variation (more acidic conditions), sea-surface temperature increase and the settlement of alien species. For instance, studies undertaken at the Prince Edward Islands, in the Indian sector of the Southern Ocean, have all reported a rise of over 1°C in sea-surface temperature since 1949 (Mélice et al., 2003; Ansorge et al., 2009, 2014). Climate change may generate favourable conditions for introduced species and cause marine biodiversity alterations (Smith, 2002; Pendlebury and Barnes-Keoghan, 2007; Schofield et al., 2010; Allan et al., 2013; Kargel et al., 2014; Molinos et al., 2015; Byrne et al., 2016). Isolated in the southern Indian Ocean, the Kerguelen Islands emerge from the Kerguelen–Heard Plateau and stand on the ACC, at the convergence between several water masses; Antarctic surface water (AASW), sub-Antarctic (SASW) and sub-Tropical (STSW) waters (Weimerskirch et al., 2003; Murphy et al., 2017). This will likely lead to the coasts being bathed by waters of different temperature, salinity, plankton and nutrient contents and will impact nearshore ecosystem properties and functioning. In this framework, knowing the actual position of the PF is important to accurately estimate the time-frame of the phenomena that will affect coastal biodiversity and ecosystem functioning. Freeman and Lovenduski (2016) indicate its latitudinal position spanning from 44° to 64°S along its circumpolar path. For Park et al. (2014), the PF location, around the Kerguelen Islands, would correspond to the northern limit of the subsurface 2°C isotherm. Due to its proximity to the Kerguelen Islands, significant changes are expected in marine life conditions (Scheffer et al., 2016).

The need for long-term ecological monitoring of coastal areas

In 2006, the National Nature Reserve of the French Southern Territories (RNN-TAF) was created by a French inter-ministerial decree (decree No. 2006-1211 of 3 October 2006). Recently, a second ministerial decree (No. 2016-1700 of 12 December 2016) has extended the RNN-TAF to most of the French exclusive economic zone (EEZ). For the Kerguelen Islands alone, the area covered by the Marine Protected Area (MPA) of the RNN-TAF was 4 998 km² in 2006, it has been significantly enlarged to reach 389 829 km² in 2016. In addition to the extension of the Kerguelen MPA, all the coastal marine area has now gained the status of enhanced protection. As a consequence, nature managers of the RNN-TAF are in need of new scientific data to support relevant conservation planning.

Since the discovery of the Kerguelen Islands, marine coastal habitats have been little impacted by direct anthropogenic disturbance (Lecomte et al., 2013). They still represent pristine marine ecosystems that are potentially important sentinels of climate change. Significant impacts of climate change can be expected on local benthic communities in which many species have limited resilience ability (Stenni et al., 2017; Gutt et al., 2018; Cárdenas et al., 2018). Environmental data must be continuously recorded for interpreting ecological changes, predicting their potential impacts on marine life and setting up relevant management plans. Such objectives can only be achieved by implementing a long-term and cross-disciplinary observing system of ecological changes (Kennicutt et al., 2016; Gutt et al., 2018). For this purpose, the IPEV program No. 1044 PROTEKER was conceived as a multidisciplinary approach including measurements of abiotic factors, benthic surveys and biological analyses (Féral et al., 2016). The objectives of the program are to identify, monitor and predict changes in marine coastal ecosystems as a basis for vulnerability assessments and appropriate management planning. The program will also contribute to the international network of nearshore observing systems of the Southern Ocean.

Material and methods

Monitored sites

The best way to investigate the macrobenthos of shallow coastal zones is SD. It can be used to: (i) determine the abundance and biomass of fauna and flora of hard bottoms (Beekley and Branch, 1992, in Marion Island), and (ii) perform pluriennial monitoring (Schories and Niedzwiedz, 2012).

During the austral summers of 2011 to 2014, three field campaigns were led along the coasts of the Kerguelen Islands to identify and equip suitable sites for monitoring. Eighteen sites off the main island, already used in the framework of previous programs, were revisited by scuba diving for photo and video surveys, looking for the best spots to set up loggers and settlement plots. Explorations were pushed down to 50 and 100 m depth in the vicinity of each site using a beam trawl and a remotely operated vehicle (ROV). Finally, eight sites were selected in different geographic areas as representative of the different Kerguelen coastal habitats. Four sites were chosen in Baie du Morbihan: Ile Haute (49°23'15"S 69°56'29"E), Ile Longue (49°32'19"S 69°53'03"E), Ilot Channer (49°22'59"S 70°11'08"E) and Ile Suhm (49°29'36"S 70°09'41"E), two in the north: Port Christmas (48°40'55"S 69°01'58"E) and Ilot des Trois Bergers (49°17'24"S 69°42'41"E), and two in the south: Fjord des Portes Noires (49°29'39"S 69°08'58"E) and Ile du Prince de Monaco (49°36'00"S 69°14'23"E) (Figure 1). The sites were marked on the shore, vertically to the installed devices, to be easily found on sight, as well as underwater at the sensors.

Equipment

Temperature loggers

HOBO® Water Temp Pro v2 loggers were selected for temperature measurements. They have a capacity of 42 000 measurements over a six-year period at the rate of one measurement per hour. Precision of sensors as specified by the manufacturer is $\pm 0.2^{\circ}\text{C}$, which is acceptable for waters with temperature variation of several degrees a year. The loggers are equipped with an optic USB interface for rapid data readout. Drift is estimated to be at $0.1^{\circ}\text{C yr}^{-1}$. Tests performed at the laboratory showed that after two years in the field, drift and precisions of loggers were of $\pm 0.1^{\circ}\text{C}$. Loggers were set up in a protective PVC box, attached to

a threaded rod, and attached to the substratum at 5 and 15 m depth, at eight different sites (Féral et al., 2016).

Conductivity loggers

During the summer campaign 2017/18, four HOBO® U-24 C loggers were installed at four sites in Baie du Morbihan for conductivity (salinity) and temperature measurements (Figure 1). The loggers were set up in a protective PVC housing to provide protection from debris and fouling while allowing water to move freely in and out. They were attached to a threaded rod, and attached to the substratum at 10 m depth, next to settlement plots (see below). They have a capacity of 18 500 measurements over a two-year period at one measurement per hour. They are ideal for detecting weak conductivity variations of $\pm 5\,000\ \mu\text{S}/\text{cm}$, and have a precision of $2\ \mu\text{S}/\text{cm}$. Temperature is routinely measured by U-24 C loggers with a precision of $\pm 0.1^\circ\text{C}$. The loggers are equipped with an optic USB interface for rapid data readout. They were set up for one conductivity and temperature measurement per hour. To calibrate the loggers and correct for the expected drift of conductivity measurements (12% per month), conductivity is also measured at the start and end of logger deployment using a WTW® 3100 portable probe.

Settlement plots

Using artificial substratum for analysing colonisation processes, growth dynamics of sessile organisms and assemblages under changing environmental conditions has proven to be a valuable and handy technique (Sutherland, 1974), including in the Southern Ocean (Stanwell-Smith and Barnes, 1997; Bowden, 2005; Bowden et al., 2006; Stark, 2008). In this study, combining settlement plots with temperature and conductivity loggers allows annual monitoring of colonisation processes with regard to year-round temperature and salinity variations. Eight $20 \times 20\ \text{cm}$ clay plots were deployed in two rows of four units on a stainless steel support, which was attached to the substratum at each monitored site. All plots are independent from each other and can be removed individually following a precise protocol (Féral et al., 2016). Settlement plots are to be exchanged yearly to generate time series of settlement dynamics. After one year, a first plot is exchanged; it will provide data after a

one-year-long settlement and community development period. After two years, the exchanged plot and a two-year old plot are sampled to have a replicate of the one-year-long experiment and data for a two-year-long settlement experiment. The process is renewed each year (see Féral et al., 2016 for more details). Results should allow: (i) assessment of the different stages of the colonisation process (succession of fouling communities) over at least an eight-year-long period, including replicates for the first four years (i.e. nine replicates of one-year plots, six of two-year plots, three of three-year plots and two of four-year plots), and (ii) evaluate spatial and temporal variation in the settlement dynamics.

When recovered, settlement plots are maintained in sea water then fixed in 95% ethanol after being photographed and cleaned off the largest organisms, which are preserved separately. Each plot is labelled, individually packed with care in a container, and sent to the laboratory for analyses in mainland France. Richness and density of sessile organisms have been assessed macroscopically using the dedicated image processing software photoQuad (Trygonis and Sini, 2012). Analyse will be completed by metabarcoding using DNA-based identification and high-throughput DNA sequencing.

Species inventory and distribution

Photo and video surveys of the monitored sites were taken to characterise benthic communities and habitats. The inventory of marine species was done by target sampling of key organisms (abundant, common, and structuring species of echinoderms, molluscs, decapods, fish and macroalgae) and associated to phylogeographic analyses to characterise the genetic structures and infer the biogeographic origin and evolution of these target species. The purpose is also to assess the role of life-history traits (reproduction mode and dispersal capacities) in the genetic structure of populations, connectivity and population dynamics conditioning the sensitivity of species to environmental changes.

Results

Environmental settings at the monitored sites

Photo and video surveys performed at each site allow determination of the main distinguishing

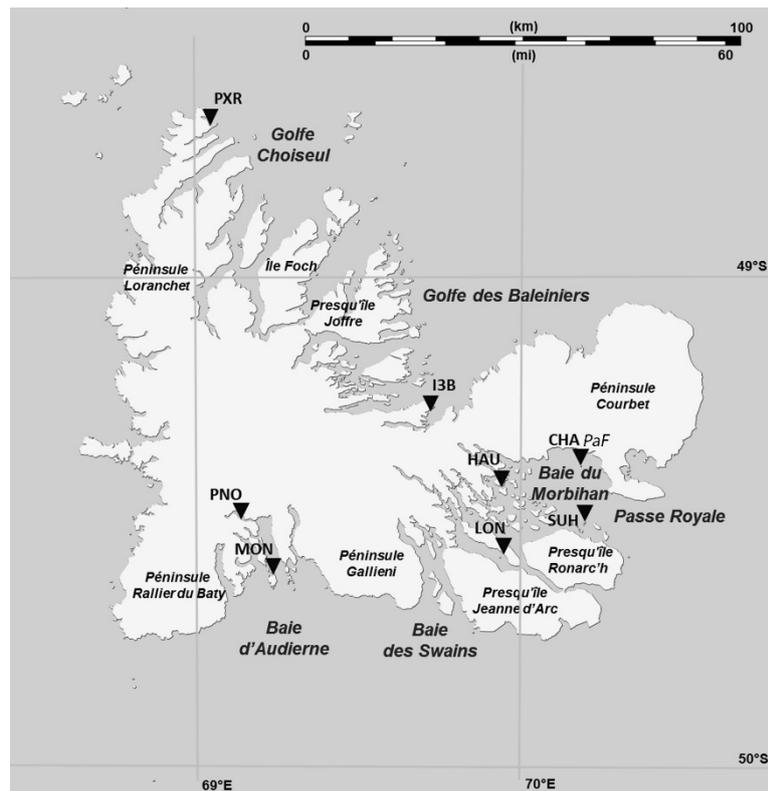


Figure 1: Map of the monitored sites (triangles): Sector Morbihan (HAU: Ile Haute, LON: Ile Longue), Passe Royale (CHA: Ilot Channer (South of Port-aux-Français, PaF), SUH: Ile Suhm), Audierne (PNO: Fjord des Portes Noires, MON: Ile du Prince de Monaco), Choiseul (PXR: Port Christmas), Baleiniers (I3B: Ilot des Trois Bergers, a small islet facing Port Couvreur).

features between sites. In particular, three taxa seem to play a key role in the composition and richness of the respective benthic communities: polychaetes, ascidians and bryozoans. To a lesser extent, sponges, sea stars and holothuroids markedly differ between sites as well. Finally, the monitored sites can differ by the local abundance of bivalves, crustaceans (amphipodes and isopodes) and ascidians.

Ile Haute (49°23'15"S 69°56'29"E) is located at the very end of Baie du Morbihan. The kelp forest of *Macrocystis pyrifera* is densely developed between 6 and 8 m depth. Kelp holdfasts become progressively sparse in deeper parts, especially on the muddy bottom. A tremendous number of sea cucumbers (*Pentactella laevigata*) are attached to kelp stipes and fronds with tentacles deployed to capture the abundant plankton and the suspended particles. The shallow underwater wall is totally covered with sessile invertebrates. In deeper parts, soft bottoms are characterised by the abundance of white sea-anemones and small colonies of ascidians. There are few arthropods and bivalves, but gastropods are well represented.

The site of Ile Longue (49°32'19"S 69°53'03"E) is located on the southwest coast of the island, on the opposite side of the Port Jeanne d'Arc Peninsula in the Passe de Buenos-Aires. Therefore, this site has not recently been exposed to the impact of the maritime traffic generated by the former sheep farm. The submarine landscape is similar to that of Ile Haute except for the high abundance and diversity of sponges that are set in the scree and in caves at the base of drop-offs that constitute shelters to some fish (*Notothenia*).

Ilot Channer (49°22'59"S 70°11'08"E) is an islet close to Port-aux-Français station. The site was chosen because it is in the main flow of the current entering Baie du Morbihan. Without big walls, it presents a chaos of blocks gradually descending towards a basin with a muddy bottom. The site is densely covered with the kelp *M. pyrifera* as in other open sea sites. Very dense at the coast, the kelp forest clears up towards the open sea. The site is characterised by a high diversity of sponges, although less densely present than at Ile Longue.

Ile Suhm (49°29'36"S 70°09'41"E) is located on the other side of the Passe Royale, facing the Ilot Channer, on a relatively sheltered drop, very rich in sponges and tunicates. The difference with previous sites is that the drop-off extends to a depth of greater than 20 m. The site is densely covered with a diverse fauna and flora that makes the site spectacular and unique compared to other sites.

Port Christmas (48°40'55"S 69°01'58"E) is located in Baie de l'Oiseau in the far north of the Kerguelen Islands. The site was chosen in a sheltered place. The kelp *M. pyrifera* also forms dense patches with some holdfasts that were torn off by storms. The walls of the drop-offs are mainly distinguished from other sites by the presence of abundant gorgonians (*Onogorgia nodosa*). Icefish (Channichthyidae) are often observed and the Antarctic horsefish (*Zanclorhynchus spinifer*) (Congiopodidae) is sometimes sighted.

Ilot des Trois Bergers (49°17'24"S 69°42'41"E) is close to Port Couvreur, in the Bras de la Fondrie (northern Kerguelen). This very small islet is characterised by a vertical drop-off that goes down to 35–40 m depth. The wall is covered with a fauna that is less diversified than the sites of Baie du Morbihan. Sea urchins (*Sterechinus diadema* and *Ctenocidaridaris nutrix*) and the giant starfish (*Labidiaster annulatus*) are commonly observed, whereas they are more common in deeper waters (50 to 100 m) at other sites.

The site of Fjord des Portes Noires (49°29'39"S 69°08'58"E) was set up beyond the fjord sill. It is characterised by freshwater inflows from rivers and melting glaciers. Measurements carried out in 2014 show the existence of a layer of low-salinity water (33.3 g kg⁻¹ on the surface increasing to 33.8 g kg⁻¹ at 10 m, to remain at 34.0 g kg⁻¹ down to 30 m). The sedimentation rate is intense, and water is often loaded with particles. The kelp *M. pyrifera* is sparsely developed. Bottoms and walls are very muddy. The large ribbed mussel *Alaucomya atra* forms a thick fringing reef there, which covers the walls and all boulders present at the site. This reef shows a significant settlement rate as deduced from the temperature loggers that are entirely covered with mussels every year. The site is also distinguished by the abundance of echinoderms, including suspension-feeding holothuroids (*P. laevigata* and abundant *Cladodactyla sicinski*), echinoids (*S. diadema*) and asteroids (*Glabraster antarctica*, *L. annulatus*).

Ile du Prince de Monaco (49°36'00"S 69°14'23"E) is located in the Bay of Audierne (southern coast of Kerguelen) and is largely exposed to the open sea. It is characterised by a well-developed kelp forest, bathing in clear and often turbulent waters. Many kelp holdfasts are regularly torn off by storms and float above the bottom. The stands are less densely covered with sessile organisms than in other, more sheltered sites (Baie de l'Oiseau, especially Baie du Morbihan). Filamentous macroalgae (cf. *Demastereias cordalis*) can have a rapid and very important seasonal development and cover very large areas.

Sea water temperature and salinity

Only temperature has been currently and continuously measured at most sites. Data are posted on www.proteker.net and updated yearly after each campaign. Due to time lags between logger deployments that have been achieved over several summer campaigns and adverse meteorological conditions, there are several gaps in temperature datasets for certain sites. Data obtained so far document seasonal variation and differences between sites and years (Figure 2). Interestingly, temperatures recorded at 5 and 15 m depth often show only slight variation at all sites, indicating an overall weak stratification of water masses, except for higher daily variation at 5 m depth.

A regular seasonal cycle of temperature variation has been observed. Overall, the highest temperature amplitudes were measured in Baie du Morbihan, particularly at Ile Haute and Ile Longue. Temperature ranges reached up to 8°C between summer maximums and winter minimums in Baie du Morbihan at 5 m depth and up to 7°C at 15 m depth. Maximum values recorded in Baie du Morbihan at Ile Longue were 9.3°C at 5 m and 8.6°C at 15 m in February 2017. Seasonal variation was lower outside the bay, ranging from 3° to 6°C for both depths. At Port Christmas, maximums only reach 5.7 ± 0.2°C, and 7.2 ± 0.2°C at Ilot des Trois Bergers. Overall, minimum values were similar inside and outside the bay. The average minimum is 2.1 ± 0.7°C at Ile Longue, in the bay, 2.7 ± 0.5°C at Port Christmas and 2.4 ± 0.8°C at Ilot des Trois Bergers outside the Bay. However, the lowest values were recorded in the bay at Ile Longue in August 2014, with 1.1°C and 1.2°C at 5 and 15 m respectively.

During three successive winter seasons (2012–2014), minimum temperature decreased

by one degree a year (3° to 1°C) then increased again to 2.5°C in winter 2015. Since 2015, winter minimums remain stable between years and close to the situation observed in 2011/12. In contrast, events of high positive anomalies now occur in the summer, in February, since 2014. Peaks were the highest at Ile Haute, Ile Longue and Fjord des Portes Noires, and to a lesser extent at Ilot Channer, slightly offbeat at Ilot des Trois Bergers (since 2012), very weak in Port Christmas and totally absent at Ile Suhm. Figure 2 illustrates two sites (Ile Longue and Ilot des Trois Bergers – see also www.proteker.net/-Thermorecorders-.html). At Ilot des Trois Bergers, temperature was particularly irregular during summer. Sudden temperature rises of several degrees took place repeatedly over a few days; they have been observed every year, from September to April. Conversely, a very continuous and regular cooling has been recorded from April (Figure 2). Temperature data are available at www.proteker.net/-Thermorecorders-.html. Since 2017, conductivity meters have been installed at several sites to continuously record variations in salinity and data will be published online on the PROTEKER website.

Colonisation dynamics on settlement plots

Settlement plots (Figure 3) could not be exchanged yearly at all sites outside Baie du Morbihan due to logistic issues, and the recovery protocol should have been modified at these sites. Furthermore, certain plots have been pulled off by strong winter storms and could not be recovered at the more exposed sites (Iles du Prince de Monaco). However, after several years, the recovery of settlement plots allows assessment of colonisation dynamics at the different sites based on image analysis with the photoQuad software.

Unexpectedly, preliminary results obtained for most sites indicate that colonisation of plots has been a relative slow and uneven process through time (Figure 4), especially during the first year, while pioneer species such as encrusting ascidians are present at all sites after two years (Figure 5). This contrasts with the very thick (usually over one decimeter) cover of organisms encrusting the rocky bottom around the plots at most sites and highlights the relatively slow dynamic of sessile community settlement and growth in cool waters of the Kerguelen Islands. However, some sites slightly differ from this general pattern. The highest colonisation

rate was observed at Ile Suhm (Figures 3 and 5), at the entrance of Baie du Morbihan, where the dense cover of biota on settlement plots could hardly be distinguished from the surrounding rocky bottom after one year. But species richness is similar to other sites and remains low compared to the community present on the rocky bottom. In contrast, at certain sites like Ilot Channer in the bay, Fjord des Portes Noires, Iles du Prince de Monaco, and Port Christmas outside the bay, settlement plots were almost bare of any sessile organisms after one year, encrusting red algae being the main organisms present. Colonisation also differs between sites with regards to pioneer organisms. At Ile Suhm and Ile Longue, the fauna includes large (up to 10 cm high) pedonculate synascidians and/or sea weeds after one year (Figure 5), while at other sites, most encrusting synascidians started colonising only after two years (Ile Haute). Overall, filamentous seaweeds were present on plots at most sites after one year, while they remain absent at certain sites, even after several years (Ile Haute). After several years, sessile assemblages are almost evenly diversified at most sites (Figure 4), but in year 3 (2016) a decrease in species richness was observed at most sites along with a decrease in the percentage of cover at certain sites (Figure 4).

Species inventory and distribution

Beyond the species inventory performed annually during the summer campaigns that permit to improve the occurrence register of numerous taxa in the Kerguelen archipelago (Figure 6), PROTEKER aims to improve our understanding about the geographic distribution of target taxa using molecular approaches. Specimens collected around Kerguelen were included in large phylogenetic and phylogeographic surveys at the scale of the Southern Ocean (González-Wevar et al., 2017, 2019a, 2019b). Such studies permit the identification of the different evolutionary units present in a genus and their geographic boundaries, and therefore the evaluation of the endemism status of these taxa on the Kerguelen Plateau. Molecular studies achieved in the framework of the PROTEKER program have demonstrated contrasting results regarding the coastal marine fauna of the Kerguelen Archipelago.

Some taxa, such as the common sea urchin *Abatus*, the bivalve *Aequiyoldia* and the Patellogastropod *Nacella* conform monophyletic groups clearly separated from other sub-Antarctic and

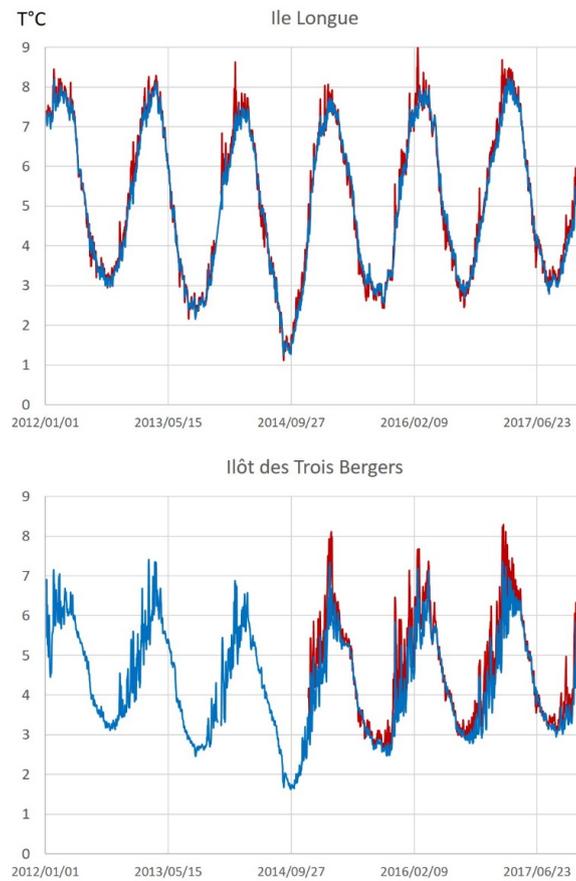


Figure 2: Raw seawater temperature at 5 m (red lines) and 15 m (blue lines) depth recorded over six years at high temporal resolution (hour) at Ile Longue and Ilôt des Trois Bergers from January 2012 to December 2017.

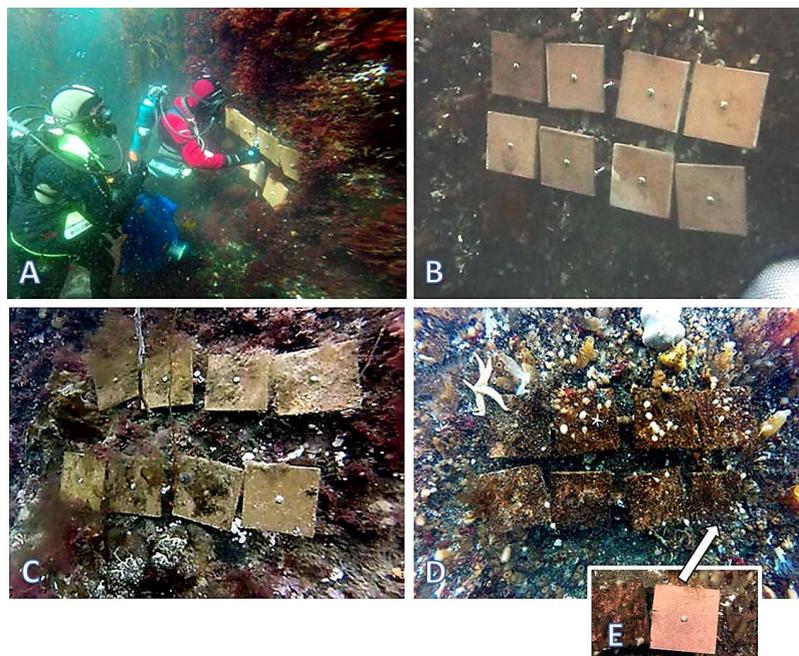


Figure 3: Settlement plots: (A) at Ilôt Channer, (B) at Ile Suhm, December 2013, (C) at Ile Haute, in December 2014, after one year, (D) at Ile Suhm, December 2014, (E) at Ile Suhm – new plot exchanged with a colonised one. Figures (C) and (D) show the strong contrast in the rate of colonising process between monitored sites.

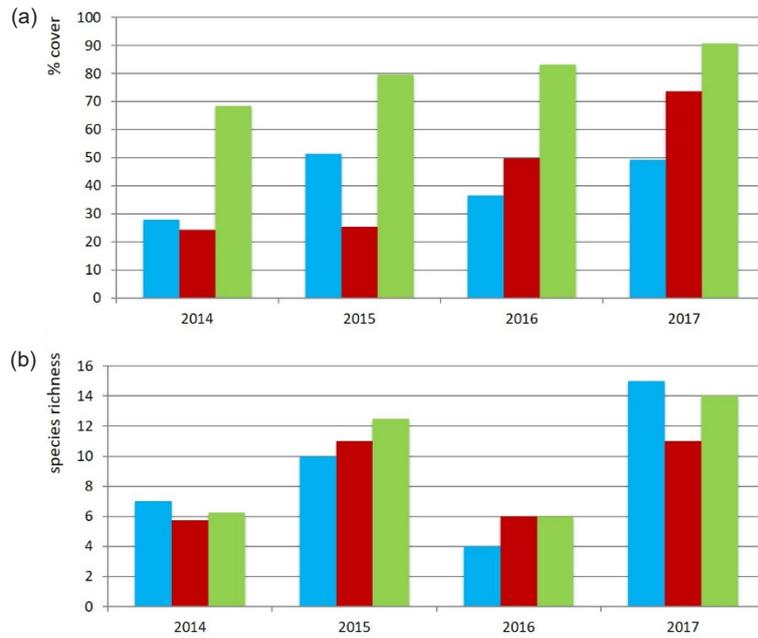


Figure 4: Colonisation dynamics on 1-year (2014), 2-year (2015), 3-year (2016) and 4-year (2017) plots, at three monitored sites of Baie du Morbihan, Ile Haute (blue), Ile Longue (red) and Ile Suhm (green), over four years (2014–2017). (a) Percentage of surface covered, (b) species richness. Values obtained from image analysis with the photoQuad software.

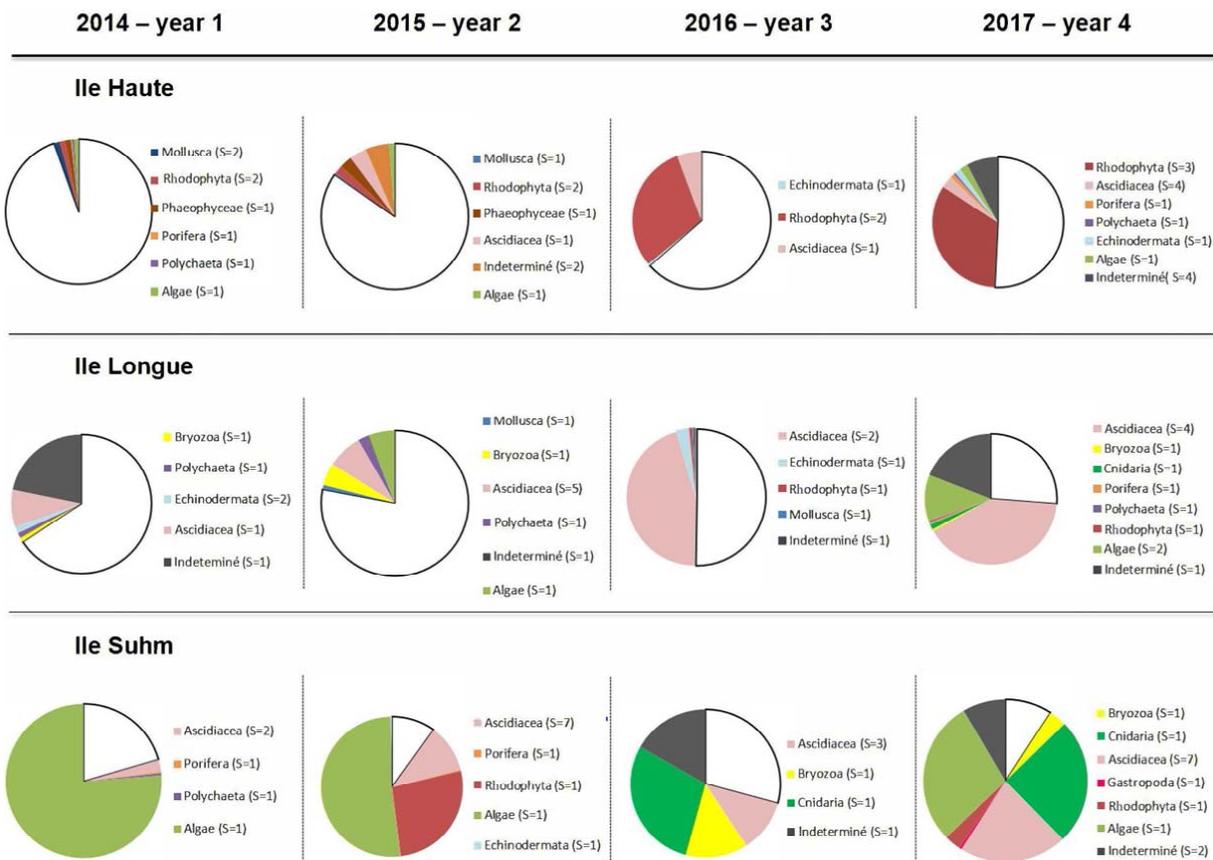


Figure 5: Colonisation patterns on 1-year (2014), 2-year (2015), 3-year (2016) and 4-year (2017) plots at three monitored sites of Baie du Morbihan, Ile Haute (blue), Ile Longue (red) and Ile Suhm (green), over four years (2014-2017). Species richness (S) and percentage of cover are displayed for each taxon. Percentage of bare surface is shown in white. Values obtained from image analysis with the photoQuad software.

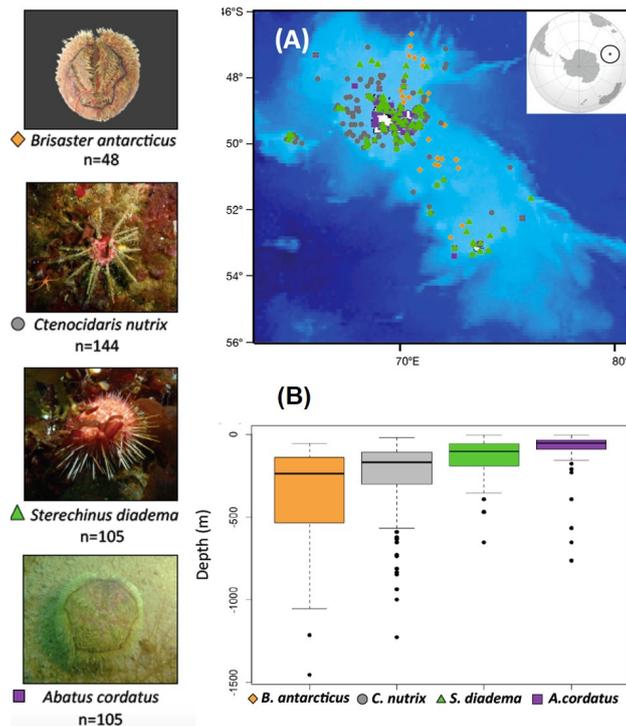


Figure 6: Distribution of four common echinoid species of the Kerguelen Plateau. (A) Map showing occurrence data of the echinoids *Brisaster antarcticus* (orange diamond), *Ctenocidaris nutrix* (grey circle), *Sterechinus diadema* (green triangle) and *Abatus cordatus* (purple square) with record numbers (n). (B) Species depth range over the Kerguelen Plateau based on occurrence data (solid line: median, box: upper and lower quartiles, whiskers: 75% ± 1.5 interquartile range, dots: outliers). The species *A. cordatus* is endemic to the Kerguelen Plateau and mostly present in shallow coastal areas (modified from Guillaumot et al., 2018).

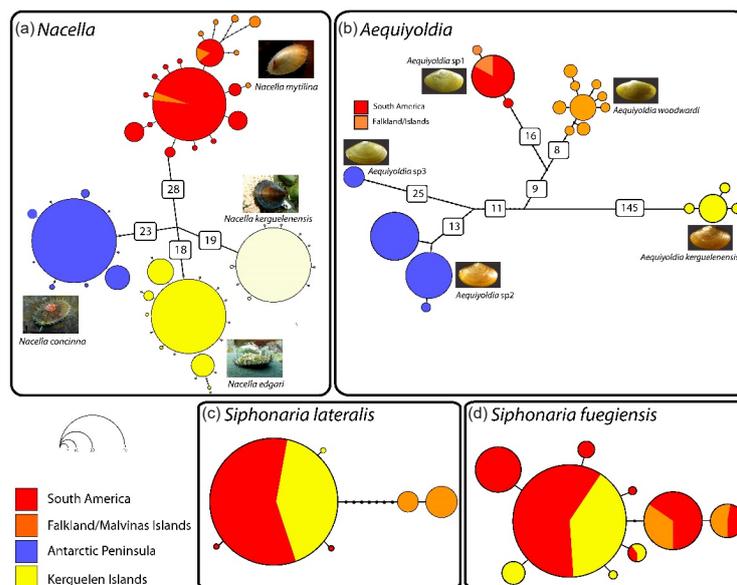


Figure 7: mtDNA (COI) maximum parsimony networks constructed in: (a) *Nacella*, (b) *Aequiyoldia*, (c) *Siphonaria lateralis*, and (d) *Siphonaria fuegiensis*. Each haplotype is represented by a coloured circle indicating the main area where it was collected. The size of the circle is proportional to its frequency in the whole sampling effort.

Antarctic regions (Figures 7a and 7b) (González-Wevar et al., 2017, 2018, 2019 a, 2019b). In contrast, in other taxa such as the regular sea urchins *Sterechinus* and the limpet *Siphonaria*, populations (Figures 7c and 7d) found in Kerguelen belong to species widely distributed across different sub-Antarctic provinces (Díaz et al., 2011; Saucède et al., 2015; González-Wevar et al., 2018). These contrasting results show that life-history traits such as the reproduction mode (brooders versus broadcasters) are not always related to the actual dispersal potential. In limpets, geographic ranges of the broadcaster *Nacella* species are much reduced compared to direct developing *Siphonaria pulmonates*. In this case, long-distance dispersal probably mediated by kelp rafting may account for such large-distance connectivity maintaining genetic cohesiveness of the species over thousands of kilometres, from South America to Macquarie Island (González-Wevar et al., 2018).

Discussion

The need for year-long temperature monitoring

In the context of the Southern Ocean, acquiring long-term datasets to detect the annual coastal variation in sea surface temperature is challenging (Féral et al., 2016; Cárdenas et al., 2018). However, there is a crucial need for surface seawater temperature data in coastal areas where benthic communities with limited thermoregulatory abilities are particularly at risk with regard to warming (Stenni et al., 2017; Gutt et al., 2018; Cárdenas et al., 2018; Richerson et al., 2018). Fine-scale time series are required to assess the effect of environmental changes on the survival, growth and reproduction of species (Cárdenas et al., 2018). High-resolution data are also required to enhance ecological modelling, improve predictions of climate change and generate realistic scenarios of species and community responses to environmental changes, which are not always relevant in coastal areas (Kennicutt et al., 2016; Gutt et al., 2018; Cárdenas et al., 2018). In this study, high-resolution seawater temperature and salinity data are now recorded year-long at different depths and eight representative sites of the Kerguelen Islands. They are regularly compiled in a substantial dataset that has been made publicly available online (www.proteker.net) for the scientific community and conservation managers. As shown in Figure 2, temperature records showed a clear decrease in the minimum winter seawater

temperature between 2012 and 2014. While minimum seawater temperature stabilised around 3°C during the winter of 2012, we can observe that temperature dropped to 2°C during the winter of 2013 and to 1°C during the winter of 2014. Such tendency clearly observed in Figure 2 may reflect southern shift of PF during these periods of harsher climatic conditions. Oceanographic and climatic data may bring some light to the origin of this severe drop in colder seawater temperature during this period, that may affect the shallow marine benthos. Such a dataset can also be used to feed and complement the international network of observing system databases such as the SCAR program Antarctic Near-shore and Terrestrial Observing System (ANTOS; www.scar.org/ssg/life-sciences/antos). Documenting long-term trends in seawater temperature will also serve as a baseline for further biological studies such as the eco-physiological experiments that are currently carried out in the Kerguelen Islands (Féral et al., 2016; Saucède et al., 2019). Both environmental and experimental data will advantageously complement each other in enhanced ecological models and scenarios of ecosystem response to climate change (Gutt et al., 2018).

Comparison between settlement plots and the 'standardised' autonomous reef monitoring system (ARMS)

Preliminary results of species richness and composition of settlement plots during the first four years of the program showed a great variability among sites, even at a small geographic scale (Figure 5). Succession dynamics do not show any tendency until now, even if different groups showed some consistency for each site. It is probably too early to detect clear tendencies and these preliminary results show the need of longer monitoring to depict some geographic pattern.

The simple systems, composed of eight independently interchangeable plots, proved to be a good choice compared to the existing standardised systems, such as ARMS boxes (Zimmerman and Martin, 2004; Leray and Knowlton, 2015). ARMS are long-term collecting devices designed to mimic the structural complexity of coral reefs and attract colonising invertebrates and were developed by CRED (Coral Reef Ecosystem Division) in partnership with the Census of Marine Life (CoML) and the Census of Coral Reef Ecosystems

(CReefs). ARMS were developed to assess and explain the diversity, distribution, abundance, and community structure of the cryptofauna community (the most diverse community of organisms on a coral reef) at a global scale (www.pifsc.noaa.gov/cred/survey_methods/arms/overview.php). This sophisticated system is well suited for tropical environments where conditions are relatively similar to each other and stable compared to differences observed among temperate seas and even more including polar seas. These artificial reefs are designed to stay immersed for one year according to a standardised protocol (Leray and Knowlton, 2015). A European program (DEVOTES project: DEvelopment Of innovative Tools for understanding marine biodiversity and assessing good Environmental Status) tested ARMS in different European regional seas (Danovaro et al., 2016; David et al., 2019, which also takes the Red Sea into account). Under the prevailing conditions (tropical and temperate seas), which are less difficult than in the Southern Ocean, it has not always been possible to closely follow the standardised protocol. The difficulties we experienced in the Kerguelen Islands showed that it would have been even more difficult there, potentially making results more difficult to interpret. A protocol similar to ARMS was adopted for analysing the settlement plots installed at the Kerguelen Islands and gave easier access to assess the recruitment dynamics and above all, this system makes it possible to obtain replicates of several different durations at the same site for as many years as needed. Even when using a different sampling unit, the system deployed in the Kerguelen Islands presents the advantage of a homogeneous protocol for both morphological and molecular identifications and can produce comparable datasets over different geographical areas.

Conservation significance and issues

The significant extension of the MPA has important implications for the coastal area which is presently included in an enhanced protection zone. This marine area may be considered as biologically pristine because there are no human-introduced species, excepting migrating salmonids, of which the impact at sea has not been evaluated (Lecomte et al., 2013). There are no exotic species and it is mostly devoid of anthropogenic disturbance. The surrounding waters provide crucial breeding habitat for a range of birds and marine mammals, some species being listed as threatened (Pardo et al.,

2017; Weimerskirch et al., 2018 as an example), and include foraging areas for a number of land-based marine predators (Tremblay and Cherel 2000, 2003; Bearhop et al., 2006). They also provide spawning and nursery areas for a range of fishes, including commercially harvested fish species (Duhamel et al., 2005, 2011; Koubbi et al., 2018; Yates et al., 2018). From a conservation point of view it should also be noted that these waters comprise a marine ecosystem that is unique and special in itself (kelp, mussel beds and reefs, fjord – unique at this latitude), and features diverse and distinctive benthic habitats that support a range of slow growing and vulnerable species.

Climate change is a key issue for biodiversity and environmental management. The Kerguelen RNN-TAF's ecosystems are vulnerable to further climate change impacts, including: sea-level rise (Testut et al., 2006; Morrow et al., 2008), ocean water acidification (Waldbusser and Salisbury, 2014; Jewett and Romanou, 2017), increases in sea-surface temperature (Cárdenas et al., 2018), and establishment of exotic/invasive species (Byrne et al., 2016). Possessing largely intact ecosystems and being relatively devoid of anthropogenic disturbance the marine reserve is a likely source of climate change indicators. Existing and future threats to the Reserve's values can be decreased by ensuring that this area will appropriately be monitored and managed.

Program completion

Initiated in December 2011, the program was renewed for four more years (2015–2018) to achieve, complement and develop the monitoring program to analyse ecological responses of coastal marine biodiversity to climate change. The next step will consist of:

- (i) complementing monitoring at the equipped sites (equipment exchanges, observations and samplings associated to settlement plots) and recording supplementary water abiotic parameters (pH, salinity, oxygen, and turbidity). In particular, new sensors (pH, salinity, oxygen, turbidity) will be set up using a durable energy source (land-based photovoltaic/wind hybrid system).
- (ii) Benthic habitat mapping (while diving and using towed gears and ROVs) will be

continuing to analyse grown-up assemblages where settlement plots were set up. The rate and quality of recruitment processes on settlement plots will be estimated and complemented by metagenomic analyses.

- (iii) Species inventory (using diving, towed gears, and ROVs) in the vicinity of the monitored sites will be completed to publish an illustrated field guide and a database (indexing and cataloguing data, making them inter-operable, traceable and compatible with international systems, contextualising and illustrating them).
- (iv) The reinforcement of the phylogeographic, trophic and ecological analyses will be performed on target taxa. In particular, taxa with a large distribution area or conversely, endemic to the island, will be selected for analysis of population genetics and phylogeographic studies to estimate the connectivity and self-recruitment in the Kerguelen Islands.

Several studies arising out of the PROTEKER program have been published (González-Wevar et al., 2017, 2018). Outcomes of the program will contribute to improve the scientific knowledge needed to support the management plan for the coastal marine domain of the RNN-TAF. In the end, members of the RNN-TAF staff will be trained in order to take charge of the long-term monitoring of the selected sites.

Logistical support of marine research

Meeting all the aforementioned objectives implies having dedicated and relevant logistical support available for work at sea, and in particular an appropriate vessel to access the sites located outside Baie du Morbihan from which specific gears and activities (ROVs, beam trawls and diving) can be operated. Results are expected to allow the production of distribution and sensitivity models for the coastal marine biodiversity of the Kerguelen Islands with regard to the expected environmental changes. The whole system will provide conservation managers with scientific grounds for determining how coastal zones should be protected and managed. PROTEKER makes part of a larger observatory network in the Southern Ocean: it has recently joined the French INEE Antarctic and sub-Antarctic workshop area (ZATA) and the SCAR

International Action Groups ANTOS (Antarctic Near-shore and Terrestrial Observing System) and ISSA (Integrated Science for the Sub-Antarctic).

Acknowledgements

This research was supported by IPEV (program No. 1044) and by Chilean Fondecyt Regular 1151336 and PIA CONICYT ACT172065 for EP. We are indebted to the RNN-TAF for completing our team in the field with a scientific diver and having made available the semi-rigid inflated boat *Le Commerson* in Baie du Morbihan. We thank the operational teams of IPEV and TAAF for the logistics on the base of Port-aux-Français and on board the RV *Marion-Dufresne II*. We are particularly grateful to the captains and the crews of RV *La Curieuse*. Thanks are also due to R. David for installing the charting library ‘dygraphs’ on the PROTEKER website used for posting of temperature data.

References

- Albouy, C., L. Velez, M. Coll, F. Colloca, F. Le Loc’h, D. Mouillot and D. Gravel. 2014. From projected species distribution to food-web structure under climate change. *Glob. Change Biol.*, 20: 730–741, doi: 10.1111/gcb.12467.
- Allan, E.L., P.W. Froneman, J.V. Durgadoo, C.D. McQuaid, I.J. Ansorge and N.B. Richoux. 2013. Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. *Ecol. Evol.*, 3 (9): 2994–3004, doi: 10.1002/ece3.678.
- Améziante, N., M. Eléaume, L.G. Hemery, F. Monniot, A. Hemery, M. Hautecoeur and A. Dettaï. 2011. Biodiversity of the benthos off Kerguelen Islands: overview and perspectives. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d’Ichtyologie, Paris: 157–167.
- Ansorge, I.J., J.V. Durgadoo and E.A. Pakhomov. 2009. Dynamics of physical and biological systems of the Prince Edward Islands in a changing climate. *Papers and Proceedings of the Tasmanian Royal Society*, 143: 15–18.
- Ansorge, I.J.; J.V. Durgadoo and A.M. Treasure. 2014. Sentinels to climate change. The need

- for monitoring at South Africa's Subantarctic laboratory. *S. Afr. J. Sci.*, 110 (1/2): a0044, doi: org/10.1590/sajs.2014/a0044.
- Arnaud, P.M. 1974. Contribution à la bionomie benthique antarctique et subantarctique. *Téthys*, 6: 469–653.
- Bearhop, S., P. Ra, R. McGill, Y. Cherel, D.A. Dawson and J.P. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar. Ecol. Prog. Ser.*, 311: 157–164, doi: 10.3354/meps311157.
- Beekley, L.E. and G.M. Branch. 1992. A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island. *Polar Biol.*, 11: 553–563, doi: 10.1007/BF00237948.
- Bowden, D.A. 2005. Seasonality of recruitment in Antarctic sessile marine benthos. *Mar. Ecol. Prog. Ser.*, 297: 101–118, doi: 10.3354/meps297101.
- Bowden, D.A., A. Clarke, L.A. Peck and D.K.A. Barnes. 2006. Antarctic sessile marine benthos: colonisation and growth on artificial substrata over three years. *Mar. Ecol. Prog. Ser.*, 316: 1–16, doi: 10.3354/meps316001.
- Byrne, M., M. Gall, K. Wolfe and A. Agüera. 2016. From pole to pole: the potential for the Arctic seastar *Asterias amurensis* to invade a warming Southern Ocean. *Glob. Change Biol.*, 22 (12): 3874–3887, doi: 10.1111/gcb.13304.
- Cárdenas, C.A., M. González-Aravena and P.A. Santibañez. 2018. The importance of local settings: within-year variability in seawater temperature at South Bay, Western Antarctic Peninsula. *PeerJ*, 6: e4289, doi: 10.7717/peerj.4289.
- David, R., M.C. Uyarra, S. Carvalho, H. Anlauf, A. Borja, A.E. Cahill, L. Carugati, R. Danovaro, A. De Jode, J.-P. Féral, D. Guillemain, M. Lo Martire, L. Thierry De Ville d'Avray, J.K. Pearman and A. Chenuil. 2019. Lessons from photo analyses of Autonomous Reef Monitoring Structures, as tools to detect (bio-)geographical, spatial, and environmental effects. *Mar. Pollut. Bull.*, 141: 420–429, doi: 10.1016/j.marpolbul.2019.02.066.
- Danovaro, R., L. Carugati, M. Berzano, A.E. Cahill, S. Carvalho, A. Chenuil, C. Corinaldesi, S. Cristina, R. David, A. Dell'Anno, N. Dzhembekova, E. Garcès, J.M. Gasol, P. Goela, J.-P. Féral, I. Ferrera, R.M. Forster, A.A. Kurekin, E. Rastelli, V. Marinova, P.I. Miller, S. Moncheva, A. Newton, J.K. Pearman, S.G. Pitois, A. Reñé, N. Rodríguez-Ezpeleta, V. Saggiomo, S.G.H. Simis, K. Stefanova, C. Wilson, M. Lo Martire, S. Greco, S. Cochrane and A. Borja. 2016. Implementing and Innovating Marine Monitoring Approaches for Assessing Marine Environmental Status. *Front. Mar. Sci.*, 3: 213 pp, doi: 10.3389/fmars.2016.00213.
- Desbruyères, D. and A. Guille. 1973. La faune benthique de l'archipel de Kerguelen. Premières données quantitatives. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D: Sciences Naturelles*, 276: 633–636.
- Díaz, A., J.-P. Féral, B. David, T. Saucède and E. Poulin. 2011. Evolutionary pathways among shallow and deep sea echinoids of the genus *Sterechinus* in the Southern Ocean. *Deep-Sea Res. II*, 58: 205–211, doi: 10.1016/j.dsr2.2010.10.012.
- Doney, S.C., M. Ruckelshaus, J. Emmett Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, J.M. Grebmeier, A.B. Hollowed, N. Knowlton, J. Polovina, N.N. Rabalais, W.J. Sydeman and L.D. Talley. 2012. Climate Change Impacts on Marine Ecosystems, *Annu. Rev. Mar. Sci.*, 4: 11–37, doi: 10.1146/annurev-marine-041911-111611.
- Duhamel, G., N. Gasco and P. Davaine. 2005. Poissons des îles Kerguelen et Crozet. Guide régional de l'océan Austral. *Patrimoines Naturels*, 63: 1–419. ISBN: 2-85653-578-3.
- Duhamel, G. P. Pruvost, M. Bertignac, N. Gasco and M. Hauteceur. 2011. Major fishery events in Kerguelen Islands: *Notothenia rossii*, *Champocephalus gunnari*, *Dissostichus eleginoides* – Current distribution and status of stocks. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 275–286.

- Duchêne, J.-C. 1976. Recherches sur les fonds meubles circalittoraux au large de Banyuls-sur-mer: étude détaillée de *Terebellides stroemi* (Polychète sédentaire). PhD Thesis, UPMC-Paris VI: 1–276, 5 annexes.
- Féral, J.-P. 1985. Changes in analyzed organic matter and energetic content of two thin-skinned holothuroids *Leptosynapta gallienae* and *Eumolpadia violacea*, at critical stages of their life cycle. In: B.F. Keegan & B.D.S. O'Connor (Eds). *Echinodermata*, Proc. 5th Intn. Echinoderm Conf., Galway (IRL): 421–429, Balkema: Rotterdam (NL). ISBN: 978-90-6191-596-6.
- Féral, J.-P. 2002. How useful are the genetic markers in attempts to understand and to manage marine biodiversity. *J. Exp. Mar. Biol. Ecol.*, 268: 121–145, doi: 10.1016/S0022-0981(01)00382-3.
- Féral, J.-P. and P. Magniez. 1985. Level, content and energetic equivalent of the main biochemical constituent of the subantarctic molpadid holothurian *Eumolpadia violacea* (Echinodermata) at two seasons of the year. *Comp. Biochem. Physiol.*, 81A: 415–422, doi: 10.1016/0300-9629(85)90157-4.
- Féral, J.-P. and P. Magniez. 1988. Relationship between rates of oxygen consumption and somatic and gonadal size in the subantarctic echinoid *Abatus cordatus* from Kerguelen. In: R.D. Burke, M.V. Mladenov, P. Lambert and R.L. Parsley (Eds). *Echinoderm Biology*, Proc. 6th Intn. Echinoderm Conf., Victoria (CAN): 581–587. ISBN: 90-6191-755-7.
- Féral, J.-P. and E. Poulin. 2011. Kerguelen Islands: a living laboratory to understand the benthic biodiversity of the Antarctic. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 151–156.
- Féral, J.-P., T. Saucède, E. Poulin, C. Marschal, G. Marty, J.-C. Roca, S. Motreuil and J.-P. Beurier. 2016. PROTEKER: implementation of a submarine observatory at the Kerguelen islands (Southern Ocean). *Underwater Technol.*, 34 (1): 1–8, doi: 10.3723/ut.34.003.
- Freeman, N.M. and N.S. Lovenduski. 2016. Mapping the Antarctic Polar Front: weekly realizations from 2002 to 2014. *Earth Syst. Sci. Data*, 8 (1): 191–198, doi: 10.5194/essd-8-191-2016.
- Gérard, K. 2008. Phylogéographie et génétique des populations des Mytilidae de l'archipel des Kerguelen: influence de l'environnement austral sur les capacités de dispersions. PhD Thesis, Université Aix-Marseille II.
- González-Wevar, C.A., M. Hüne, N.I. Segovia, T. Nakano, H. Spencer, S.L. Chown, T. Saucède, G. Johnstone, A. Mansilla and E. Poulin. 2017. Following the Antarctic Circumpolar Current: Patterns and processes in the biogeography of the limpet *Nacella* (Mollusca: Patellogastropoda) across the Southern Ocean. *J. Biogeogr.*, 44 (4): 861–874, doi: 10.1111/jbi.12908.
- González-Wevar, C.A., N.I. Segovia, S. Rosenfeld, J. Ojeda, M. Hüne, J. Naretto, T. Saucède, P. Brickle, S. Morley, J.-P. Féral, H.G. Spencer and E. Poulin. 2018. Long-distance dispersal in higher latitude sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) species. *J. Biogeogr.*, 45 (4): 874–884, doi: 10.1111/jbi.13174.
- González-Wevar, C.A., M. Hüne, S. Rosenfeld, T. Nakano, T. Saucède, H.G. Spencer and E. Poulin. 2019a. Systematic revision of *Nacella* (Patellogastropoda: Nacellidae) based on a complete phylogeny of the genus, with the description of a new species from the southern tip of South America. *Zool. J. Linn. Soc.-Lond.*, in press, doi: 10.1093/zoolinnean/zly067.
- González-Wevar C., K. Gérard, S. Rosenfeld, E. Poulin, T. Saucède, J. Naretto, A. Díaz, S. Morley and P. Brickle. 2019b. Cryptic speciation in Southern Ocean *Aequiyoldia eightsii* (Jay, 1839): Mio-Pliocene trans-Drake separation and diversification. *Prog. Oceanogr.*, 174: 44–54, doi: 10.1016/j.pocean.2018.09.004.
- Grua, P. 1963. Plongée biologiques sous-marines aux îles St-Paul et Nouvelle Amsterdam. CNFRA, Paris, 4: 37–49.
- Grua, P. 1964a. Sur la structure des peuplements de *Macrocystis pyrifera* (L.) C. Ag. observés en plongée à Kerguelen et Crozet. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D: Sciences Naturelles*, 259: 1541–1543.

- Grua, P. 1964b. Premières données sur les biomasses de l'herbier à *Macrocystis pyrifera* de la Baie du Morbihan (Archipel Kerguelen). *La Terre et la Vie*, 2: 215–220.
- Grua, P. 1967. Lutte contre le froid et adaptation rapide aux conditions de plongée dans des eaux froides. Kerguelen 1962-63. In: Tromp, S.W. and W.H. Weihe (Eds). *Proceedings of the 3rd International Biometeorological Congress*. Pau, 1–7 September 1963. Pergamon Press, Oxford, New York: 831–836.
- Grua, P. (Ed.). 1971. Invertébrés de l'infralittoral rocheux dans l'archipel de Kerguelen. Tome I: Introduction écologique. Hydraires, Bryozoaires, Amphineures, Prosobranches, Eponges calcaires, Pycnogonides. *CNFRA*, 30: 1–66.
- Grua, P. (Ed.). 1973. Invertébrés de l'infralittoral rocheux dans l'archipel de Kerguelen. Tome II: Polychètes, Cirripèdes, Isopodes, Tanaïdacés, Décapodes, Ascidiés. *CNFRA*, 32: 1–74.
- Grua, P. (Ed.) 1974. Invertébrés de l'infralittoral rocheux dans l'archipel de Kerguelen. Tome III: Némertes, Opisthobranches, Bivalves, Amphipodes, Holothurides, Echinides, Astérides, Ophiuroïdes. *CNFRA*, 35: 1–44.
- Guillaumot, C., A. Martin, T. Saucède and M. Eléaume. 2018. Methodological clues for improving species distribution models in data-poor areas: example of sub-Antarctic benthic species on the Kerguelen Plateau. *Mar. Ecol. Prog. Ser.*, 594: 149–164, doi: 10.3354/meps12538.
- Guille, A. 1977. Benthic bionomy of the continental shelf of the Kerguelen Islands: quantitative data on the Echinoderms of the Morbihan Gulf. In: Llano, G.A. (Ed.). *Adaptations within Antarctic Ecosystems, Proceedings of the 3rd SCAR Symposium on Antarctic Biology*. Smithsonian Institution printed and distributed by Gulf Publishing Company, Book Division: 253–262.
- Guille, A. and P. Lasserre. 1979. Consommation d'oxygène de l'oursin *Abatus cordatus* (Verrill) et activité oxydative de son biotope aux îles Kerguelen. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, N.S. 43: 211–219.
- Gutt, J., E. Isla, A.N. Bertler, G.E. Bodekerd, T.J. Bracegirdle, R.D. Cavanagh, J.C. Comiso, P. Convey, V. Cummings, R. De Conto, D. De Master, G. di Prisco, F. d'Ovidio, H.J. Griffiths, A.L. Khan, J. López-Martínez, A.E. Murray, U.N. Nielsen, S. Ott, A. Post, Y. Ropert-Coudert, T. Saucède, R. Scherer, S. Schiaparelli, I.R. Schloss, C.R. Smith, J. Stefels, C. Stevens, J.M. Strugnell, S. Trimborn, C. Verde, E. Verleyen, D.H. Wall, N.G. Wilson and J.C. Xavier. 2018. Cross-disciplinarity in the advance of Antarctic ecosystem research. *Mar. Genom.*, 37: 1–17, doi: 10.1016/j.margen.2017.09.006.
- Hattab, T., F. Leprieur, F.B.R. Lasram, D. Gravel, F.L. Loc'h and C. Albouy. 2016. Forecasting fine-scale changes in the food web structure of coastal marine communities under climate change. *Ecography.*, 39: 1227–1237, doi: 10.1111/ecog.01937.
- Hoegh-Guldberg, O. and J.F. Bruno. 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science*, 328 (5985): 1523–1528, doi: 10.1126/science.1189930.
- Hureau J.-C. 2011. Marine research on the Kerguelen Plateau: from early scientific expeditions to current surveys under the CCAMLR objectives. In: Duhamel, G. and D. Welsford (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries*. Société Française d'Ichtyologie, Paris: 5–13.
- Jewett, L. and A. Romanou. 2017. Ocean acidification and other ocean changes. In: Wuebbles, D.J., D.W. Fahey, K.A. Hibbard, D.J. Dokken, B.C. Stewart, and T.K. Maycock (Eds). *Climate Science Special Report: Fourth National Climate Assessment*, Volume I, U.S. Global Change Research Program, Washington, DC, USA: 364–392, doi: 10.7930/J0QV3JQB.
- Kargel, J.S., A.B.G. Bush, J.G. Cogley, G.J. Leonard, B.H. Raup, C. Smiraglia, M. Pecci and R. Ranzi. 2014. A world of changing glaciers: Summary and climatic context. In: Kargel, J.S., G.J. Leonard, M.P. Bishop, A. Käab and B.H. Raup (Eds). *Global Land Ice Measurements from Space*. Springer, Berlin Heidelberg: 781–840, doi: 10.1007/978-3-540-79818-7_33.
- Kennicutt, M.C., Y.D. Kim, M. Finnemore-Rogan, S. Anandakrishnan, S.L. Chown, S. Colwell,

- D. Cowan, C. Escutia, Y. Frenot, J. Hall, D. Liggett, A. McDonald, U. Nixdorf, M.J. Siegert, J. Storey, A. Wåhlin, A. Weathewax, G.A. Wilson, T. Wilson, R. Wooding, S. Ackley, N. Biebow, D. Blankenship, S. Bo, J. Baesemann, C.A. Cárdenas, J. Cassano, C. Danhong, J.J. Dañobeitia, J. Francis, J. Guldahl, G. Hashida, L. Jimenz Corbalan, A. Klepikov, J. Lee, M. Leppe, F. Lijun, J. López-Martinez, R. Memolli, Y. Motoyoshi, R. Mousalle Bueno, J. Negrete, M.A. Ojeda Cárdenas, M. Proaño Silva, S. Ramos-Garcia, H. Sala, P. Sheppard, H. Shin, X. Shijie, K. Shiraishi, T. Stockings, S. Trotter, D.J. Vaughan, J. Viera Da Unha De Menezes, V. Vlasich, Q. Weijia, J.-G. Winthers, H. Miller, S. Rintoul and H. Yang. 2016. Delivering 21st century Antarctic and Southern Ocean science. *Ant. Sci.*, 28: 407–423, doi: 10.1017/S0954102016000481.
- Koubbi, P., C. Guinet, N. Alloncle, N. Ameziane, C.S. Azam, A. Baudena, C.A. Bost, R. Causse, C. Chazeau, G. Coste, C. Cotté, F. D’Ovidio, K. Delord, G. Duhamel, A. Forget, N. Gasco, M. Hauteœur, P. Lehodey, C. Lo Monaco, C. Marteau, A. Martin, C. Mignard, P. Pruvost, T. Saucède, R. Sinagre, T. Thellier, A.G. Verdier and H. Weimerskirch. 2018. Ecoregionalisation of the Kerguelen and Crozet islands oceanic zone. Part I: Introduction and Kerguelen oceanic zone. Document *WG-EMM-16/43*. CCAMLR, Hobart, Australia, doi: 10.13140/RG.2.2.17278.18246.
- Lecomte, F., E. Beall, J. Chat, P. Davaine and P. Gaudin. 2013. The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biol.*, 36: 457–475, doi: 10.1007/s00300-012-1281-5.
- Leray, M. and N. Knowlton. 2015. DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. *P. Natl. Acad. Sci. USA*, 112 (7): 2076–2081, doi: 10.1073/pnas.1424997112.
- Le Roux, P.C. and M.A. McGeoch. 2008. Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change*, 86: 309–329, doi: 10.1007/s10584-007-9259-y.
- Loreau, M. and N. Behera. 1999. Phenotypic Diversity and Stability of Ecosystem Processes. *Theor. Popul. Biol.*, 56: 29–47, doi: 10.1006/tpbi.1998.1408.
- Magniez, P. 1980. Modalité de l’incubation chez *Abatus cordatus*, oursin endémique des Iles Kerguelen. In: Jangoux, M. (Ed.) *Echinoderms: Present and Past*. Proceedings of the European Colloquium on Echinoderms, Brussels (BE). Balkema, Rotterdam: 399–403. ISBN: 90 6191 077 3.
- Magniez, P. 1983. Reproductive cycle of the brooding echinoid *Abatus cordatus* (Echinodermata) in Kerguelen (Antarctic Ocean): changes in the organ indices, biochemical composition and calorie contents of the gonads. *Mar. Biol.*, 74: 55–64, doi: 10.1007/BF00394275.
- Magniez, P. and J.-P. Féral. 1988. The effect of somatic and gonadal size on the rate of oxygen consumption in the subantarctic echinoid *Abatus cordatus* (Echinodermata) from Kerguelen. *Comp. Biochem. Physiol.*, 90A: 429–434, doi: 10.1016/0300-9629(88)90214-9.
- Mélice, J.L., J.R.E. Lutjeharms, M. Rouault and I.J. Ansorge. 2003. Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *S. Afr. J. Sci.*, 99: 363–366.
- Mespoullhé, P. 1992. Morphologie d’un échinide irrégulier subantarctique de l’Archipel des Kerguelen: Ontogenèse, dimorphisme sexuel et variabilité. Thèse, Université de Bourgogne: 1–184.
- Molinos, J.G., B.S. Halpern, D.S. Schoeman, C.J. Brown, W. Kiessling, P.J. Moore, J.M. Pandolfi, E.S. Poloczanska, A.J. Richardson and M.T. Burrows. 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nat. Clim. Change*, 6 (1): 83–88, doi: 10.1038/nclimate2769.
- Morrow, R., G. Valladeau and J.-B. Sallee. 2008. Observed subsurface signature of Southern Ocean sea level rise. *Prog. Oceanog.*, 77: 351–366, doi: 10.1016/j.pocean.2007.03.002.
- Murphy, E.J., S.E. Thorpe, G.A. Tarling, J.L. Watkins, S. Fielding and P. Underwood. 2017. Restricted regions of enhanced growth of

- Antarctic krill in the circumpolar Southern Ocean. *Scientific Reports*, 7: 6963, doi: 10.1038/s41598-017-07205-9.
- Pardo, D.; S. Jenouvrier, H. Weimerskirch and C. Barbraud. 2017. Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. *Phil. Trans. R. Soc. Lond. B*, 372: 20160143, doi: 10.1098/rstb.2016.0143.
- Park, Y.H., I. Durand, E. Kestenare, G. Rougier, M. Zhou, F. d'Ovidio, C. Cotte and J.H. Lee. 2014. Polar Front around the Kerguelen Islands: An up to-date determination and associated circulation of surface/subsurface waters. *J. Geophys. Res-Oceans*, 119 (10): 6575–6592, doi: 10.1002/2014JC010061.
- Pendlebury, S.F. and L.P. Barnes-Keoghan. 2007. Climate and climate change in the sub-Antarctic. *Papers and Proceedings of the Royal Society of Tasmania*, 141 (1): 67–82.
- Poulin, E. 1996. Signification évolutive et conséquences de l'incubation chez un invertébré marin benthique subantarctique, *Abatus cordatus* (Verrill, 1876) (Echinodermata: Spatangoida). Thèse, Université Montpellier II: 1–186, 12 annexes.
- Poulin, E. and J.-P. Féral. 1995. Pattern of spatial distribution of a brood-protecting schizasterid echinoid, *Abatus cordatus*, endemic to the Kerguelen Islands. *Mar. Ecol. Prog. Ser.*, 118: 179–186, doi: 10.3354/meps118179.
- Poulin, E. and J.-P. Féral. 1996. Why are there so many species of brooding Antarctic echinoids? *Evolution*, 50: 820–830, doi: 10.2307/2410854.
- Poulin E., A.T. Palma and J.-P. Féral. 2002. Evolutionary versus ecological success of developmental modes in coastal Antarctic benthic invertebrates. *Trends Ecol. Evol.*, 17: 218–222, doi: 10.1016/S0169-5347(02)02493-X.
- Richerson, K., R. Driscoll and M. Mangel. 2018. Increasing temperature may shift availability of euphausiid prey in the Southern Ocean. *Mar. Ecol. Prog. Ser.*, 588: 59–70, doi: 10.3354/meps1246.
- Rouault, M., J.-L. Mélice, C.J.C. Reason and J.R.E. Lutjeharms. 2005. Climate variability at Marion Island, Southern Ocean, since 1960. *J. Geophys. Res.*, 110: C05007, doi: 10.1029/2004JC002492.
- Saucède, T., A. Diaz. B. Pierrat. J. Sellanes. B. David. J.-P. Féral and E. Poulin. 2015. The phylogenetic position and taxonomic status of *Sterechinus bernasconiae* Larrain, 1975 (Echinodermata, Echinoidea), an enigmatic Chilean sea urchin. *Polar Biol.*, 38: 1223–1237, doi: 10.1007/s00300-015-1689-9.
- Saucède, T., C. Guillaumot, L.N. Michel, S. Fabri-Ruiz, A. Bazin, M. Cabessut, A. García-Berro, A. Mateos, O. Mathieu, C. De Ridder, P. Dubois, B. Danis, B. David, A. Díaz, G. Lepoint, S. Motreuil, E. Poulin and J.-P. Féral. 2019. Modelling species response to climate change in sub-Antarctic islands: echinoids as a case study for the Kerguelen Plateau. In: Welsford, D., J. Dell and G. Duhamel (Eds). *The Kerguelen Plateau: marine ecosystem and fisheries. Proceedings of the Second Symposium*. Australian Antarctic Division, Kingston, Tasmania, Australia: this volume.
- Schatt, P. 1985. Développement et croissance embryonnaire de l'oursin incubant *Abatus cordatus* (Echinoidea: Spatangoidea). PhD Thesis, UPMC-Paris VI: 1–151.
- Scheffer, A, P.N. Trathan, J.G. Edmonston and C.-A. Bost. 2016. Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Prog. Oceanogr.*, 141: 1–16, doi: 10.1016/j.pocean.2015.10.005.
- Schofield, O., H.W. Ducklow, D.G. Martinson, M.P. Meredith, M.A. Moline and W.R. Fraser. 2010. How do polar marine ecosystems respond to rapid climate change? *Science*, 328 (5985): 1520–1523, doi: 10.1126/science.1185779.
- Schories D. and G. Niedzwiedz. 2012. Precision, accuracy, and application of diver-towed underwater GPS receivers. *Environ. Monit. Assess.*, 184: 2359–2372, doi 10.1007/s10661-011-2122-7.

- Smith, V.R. 2002. Climate change in the sub-Antarctic: An illustration from Marion Island. *Climatic Change*, 52: 345–357, doi: 10.1023/A:1013718617277.
- Stanwell-Smith, D. and D.K.A. Barnes. 1997. Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. *J. Exp. Mar. Biol. Ecol.*, 212: 61–79, doi: 10.1016/S0022-0981(96)02754-2.
- Stark, J.S., 2008. Patterns of higher taxon colonisation and development in sessile marine benthic assemblages at Casey Station, Antarctica, and their use in environmental monitoring. *Mar. Ecol. Prog. Ser.*, 365: 77–89.
- Stenni, B., M.A.J. Curran, N.J. Abram, A. Orsi, S. Goursaud, V. Masson-Delmotte, R. Neukom, H. Goosse, D. Divine, T. Van Ommen, E.J. Steig, D.A. Dixon, E.R. Thomas, N.A.N. Bertler, E. Isaksson, A. Ekaykin, M. Werner and M. Frezzotti. 2017. Antarctic climate variability on regional and continental scales over the last 2000 years. *Clim. Past*, 13:1609–1634, doi: 10.5194/cp-13-1609-2017.
- Sutherland, J.P. 1974. Multiple stable points in natural communities. *Am. Nat.*, 108: 859–873, doi: 10.1086/282961.
- Testut, L., G. Woppelmann, B. Simon and P. Téchiné. 2006. The sea level at Port-aux-Français, Kerguelen Island, from 1949 to the present. *Ocean Dynam.*, 56 (5): 464–472, doi: 10.1007/s10236-005-0056-8.
- Trembaly, Y. and Y. Cherel. 2000. Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar. Ecol. Prog. Ser.*, 204: 257–267, doi: 10.3354/meps204257.
- Trembaly, Y. and Y. Cherel. 2003. Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Mar. Ecol. Prog. Ser.*, 251: 279–297, doi: 10.3354/meps251279.
- Trygonis, V. and M. Sini. 2012. PhotoQuad: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *J. Exp. Mar. Biol. Ecol.*, 424–425: 99–108.
- Tynan, C.T. 1998. Ecological importance of the southern boundary of the Antarctic Circumpolar Current. *Nature*, 392 (6677): 708–710, doi: 10.1038/33675.
- Ullah, H., I. Nagelkerken, S.U. Goldenberg and D.A. Fordham. 2018. Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. *PLoS Biology*, 16 (1): e2003446, doi: 10.1371/journal.pbio.2003446.
- Waldbusser, G.G. and J.E. Salisbury. 2014. Ocean Acidification in the Coastal Zone from an Organism's Perspective: Multiple System Parameters, Frequency Domains, and Habitats. *Annu. Rev. Mar. Sci.*, 6: 221–247, doi: 10.1146/annurev-marine-121211-172238.
- Weimerskirch, H., P. Inchausti, C. Guinet and C. Barbraud. 2003. Trends in birds and seals populations as indicators of a system shift in the Southern Ocean. *Ant. Sci.*, 15 (2): 249–256, doi: 10.1017/S0954102003001202.
- Weimerskirch, H., K. Delord, C. Barbraud, F. Le Bouard, P.G. Ryan, P. Fretwell and C. Marteau. 2018. Status and trends of albatrosses in the French Southern Territories, Western Indian Ocean. *Polar Biol.*, 41 (10): 1963–1972, doi: 10.1007/s00300-018-2335-0.
- Yates, P., P. Ziegler, D. Welsford, J. McIvor, B. Farmer and E. Woodcock. 2018. Spatio-temporal dynamics in maturation and spawning of Patagonian toothfish *Dissostichus eleginoides* on the sub-Antarctic Kerguelen Plateau. *J. Fish Biol.*, 92 (1): 34–54, doi: 10.1111/jfb.13479.
- Zimmerman, T.L. and J.W. Martin. 2004. Artificial Reef Matrix Structures (Arms): An Inexpensive and Effective Method for Collecting Coral Reef-Associated Invertebrates. *Gulf and Caribbean Research*, 16 (1): 59–64, doi: 10.18785/gcr.1601.08.