様　式　Ｃ－１９、Ｆ－１９－１、Ｚ－１９　（共通）

科学研究費助成事業　　研究成果報告書

令和　３ 年　 ６ 月 １５ 日現在

機関番号：１２１０２
研究種目：若手研究(B)
研究期間：2017～2020
課題番号：１７Ｋ１７６２２

研究課題名（和文）Understanding the Impacts of Ocean Acidification: from Biodiversity to Ecosystem Functioning

研究課題名（英文）Understanding the Impacts of Ocean Acidification: from Biodiversity to Ecosystem Functioning

研究代表者
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交付決定額（研究期間全体）：（直接経費）　　2,500,000円

研究成果の概要（和文）：現在の海洋中のCO2濃度は、海底生物が複雑な三次元的構造を作り出すのに適しており、それによって高い生物多様性が保たれています。一方、CO2濃度が高くなり海洋が酸性化すると、生物群の構成が変化する過程（遷移過程）の初期段階において、環境の変化が激しい場所でも多くの子孫を残す生存戦略をとる、微細藻や小型の藻類（日和見種）が増え、他の大型藻類の加入が阻害されます。そのため、生態系における種の多様性は低いままとなり、構造的な複雑性を持つことができません。構造的複雑性は、様々な生物資源を創出するなど、生態系の機能的側面を支えており、その喪失は、人類が享受する生態系サービスの劣化を意味しています。

研究成果の学術的意義や社会的意義
人間活動に伴い、沿岸の生態系の構造や機能が劇的に変化しています。特に、海藻の海中林やサンゴ礁がマット状の微細藻類に置き換わると、我々人類にとっての生態系の価値は著しく失われます。これから数十年で、多様で複雑性の高い環境が日和見種(短寿命で成長速度の大きな種)とされる微細藻類に置き換わるかもしれません。さらに、微細藻類が卓越すると他の生物種の加入が妨げられ、生態系の遷移が停止することも明らかとなりました。このようなフィードバックの仕組みは、様々なレベルでの環境変化に対して閾値を踏み越えた生態系の安定化を説明するものであり、沿岸生態系の価値を守るための適応戦略に組み入れることが必要です。

研究成果の概要（英文）：Long-term exposure to CO2 can considerably alter community development, often resulting in simplified systems dominated by turf algae that possess reduced biodiversity and low ecological complexity. Current understanding of the underlying processes by which ocean acidification alters biological community development and stability remains limited, making the management of such shifts problematic. Here, we found that assemblages in reference pCO2 conditions continued to gain species through time and had developed more structurally complex communities with clearly defined understory and canopy species. In contrast, the assemblages in the elevated pCO2 became arrested in terms of their successional development due to competition for space by the turf algae, resulting in a highly simplified community. By understanding the ecological processes responsible for driving shifts in community composition, we can better assess how communities are likely to be altered by ocean acidification.

研究分野：Climate Change Marine Ecology

キーワード：Ocean Acidification　Community Succession　Biodiversity　Climate Change　Meta-barcoding　Ecosystem Functioning

Title: Understanding the Impacts of Ocean Acidification: from Biodiversity to Ecosystem Functioning

１．研究開始当初の背景

Marine ecosystems are currently under threat from ocean acidification, the change in seawater carbonate conditions associated with increasing levels of atmospheric CO_2. Although some species may benefit from elevated CO_2 (e.g., some fleshy macroalgae species) - under our current rate of CO_2 emissions, most marine organisms evaluated will have very high risk of negative impacts by 2100 and many by 2050 (Gattuso et al., 2015). This variety of responses within and between taxa mean that ocean acidification is likely to drive substantial change in marine ecosystems (Agostini et al., 2018; Hall-Spencer & Harvey, 2019). While these ecosystem changes are often gradual, they can reach tipping points, resulting in dramatic and abrupt regime shifts that change the structure and function of marine communities (Conversi et al., 2015; Möllmann et al., 2015). Regime shifts are particularly concerning because they can cause large losses of ecological and economic resources, and yet are often difficult to predict due to their non-linear nature (Hastings & Wysham, 2010). Presently, the next significant knowledge gap is to understand how ocean acidification will affect the structure and functioning of whole communities, with the long-term aim of informing on the implications for the ecosystem services that these communities provide (e.g. food, habitat provisioning, coastal defense, nutrient cycling).

２．研究の目的

There has been extensive research into the effects of OA on single species (reviewed by Harvey et al., 2013, 2014), yet these experiments rarely investigate species interactions (such as habitat provisioning, competition, predation, or food limitation) and so it is difficult to assess how the results apply to natural ecosystems. By using natural *in-situ* CO_2 seeps, where CO_2 bubbles through the seabed due to nearby volcanoes, it is possible to provide insights into the future of marine ecosystems because they expose entire communities to the conditions we expect by the end of the century. This provides researchers with an avenue to assess the long-term development of communities and provides insights into whether resident species can cope or adapt to ocean acidification over their life span.

Previous work using CO_2 seeps across temperate, sub-tropical and tropical systems has shown profound shifts in the community due to ocean acidification (Hall-Spencer & Harvey, 2019), finding that ecosystems became increasingly simplified under ocean acidification with declines in biodiversity, habitat, and structural complexity. However, since these community assessments carried out to date having typically used traditional ecological methods, they have almost exclusively focussed on large and conspicuous species that represent only a minor fraction of marine diversity. Traditional approaches thereby highlight a limitation - how can we comprehensively quantify changes in biodiversity over time and understand the consequences of community shifts on ecosystem services if most species are unknown to science or cannot be easily surveyed? The purpose of this research was therefore to address this knowledge gap by using meta-barcoding approaches to characterise whole communities, link it to their ecosystem

functioning, and test how ocean acidification will influence biodiversity and ecosystem functioning.

３．研究の方法

Recruitment tiles (150 x 150 mm volcanic rock tiles) were deployed in July 2016 in Shikine Island, being secured to the substrate using individual anchor bolts (8.5 mm width, 70 mm length) drilled into rock by SCUBA divers at ~6 m depth (Nemo Underwater Drill, Nemo Power Tools, CA, USA). Tiles were deployed within two zones: (i) near to the natural CO_2 seeps (High-CO_2, 900 ppm), and (ii) in a nearby bay for control conditions (Reference, 300 ppm). A total of 50 tiles were utilised (n = 25 per zone) with a subset of five tiles collected and analysed after 2, 4, 9, 18 and 24 months. These recruitment tiles allow us to analyse the biodiversity and abundance of species under different levels of CO_2 when substrate complexity and colonisation history are being held constant.

Upon collection, each tile was removed from the substrate and placed into plastic bags underwater and transported back to the laboratory. Within the laboratory, each recruitment tile was photographed (Nikon D7200, Nikon, Japan) to assess the total percentage cover of the tile, then each tile was measured for gross primary production and community respiration in a measure of the tiles community production rate, and finally each tile was stored at -20 °C until DNA extraction.

Community production and respiration of individual tiles were assessed by measuring, with an Orion 4-Star pH and dissolved oxygen meter (Thermo Scientific, USA), the changes in dissolved oxygen concentrations during an incubation within a 2.5 L seawater container (15 cm wide x 20 cm length x 10 cm height) in a temperature-controlled water bath. Magnetic stirrers (M-1 Controller and MS101A Stirrer, AS-One, Japan) were used to continuously mix the seawater within each container throughout measurements. Seawater for each treatment (pH_{NBS} ~8.10 vs. pH_{NBS} ~7.80) were acquired by bubbling with pure CO_2 (Fukurow pH Controller; Aqua Geek, Kawaguchi, Japan). Community production and respiration were measured over a 150-minute period; first determining oxygen production (60-minute light period, *ca*. 200 μmol m^{-2} s^{-1}), and after a 30-minute dark period, oxygen consumption (60-minute dark period). Net community production and community respiration were measured during the light and dark periods, respectively, with gross primary production calculated as the net community production minus community respiration.

The DNA was extracted from each tile using a Powermax Soil DNA Isolation Kit (MO-BIO) on homogenised tissue scraped from each tile. PCR assays were used to amplify universal primers of >300-bp, COI and 18S (eukaryotic organisms) and 16S (prokaryotic organisms) fragments - in each replicate sample before being sent for sequencing. Sequences were cleaned and processed using QIIME2 with DADA2, with downstream analysis carried out in the R environment. Comparisons were made between the ‘Reference’ and ‘High-CO_2’ sites, separately for the bacterial community composition (16S), algal community composition (18S) and fauna (COI).

４．研究成果

Overall community composition between the Reference and High-CO_2 sites at all time points were highly separated by nMDS for bacteria (Figure 1A-B), algae (Figure 1C-D) and fauna (Figure 1E-F). This highlights that across early-stage (2-m and 4-m), mid-stage (9-m), and late-stage (18-m and 24m) succession, communities entirely diverge and remain separated in terms of their composition. These differences in the community are also demonstrated by diversity, with the high-CO_2 showing reduced diversity compared to the Reference site. This is most clearly shown when looking at the latest stages of succession (24-m), where assemblages in reference pCO_2 conditions continued to gain species through time and had developed more structurally complex communities with clearly defined understory and canopy species (Figure 2). In contrast, the assemblages in the elevated pCO_2 became arrested in terms of their successional development due to competition for space by the turf algae, resulting in a highly simplified community (Figure 2).

The turf algae that were observed at 24 months in the High-CO_2 site, was also prevalent at other time points, and likely played a role in maintaining the species-poor state. The benefits of seawater acidification to opportunistic species, such as turf algae, over others (including calcareous species) is well established. It is likely that the enriched CO_2 environment had a positive effect on the fast-growing microalgae and turf algal species in the early stages of community

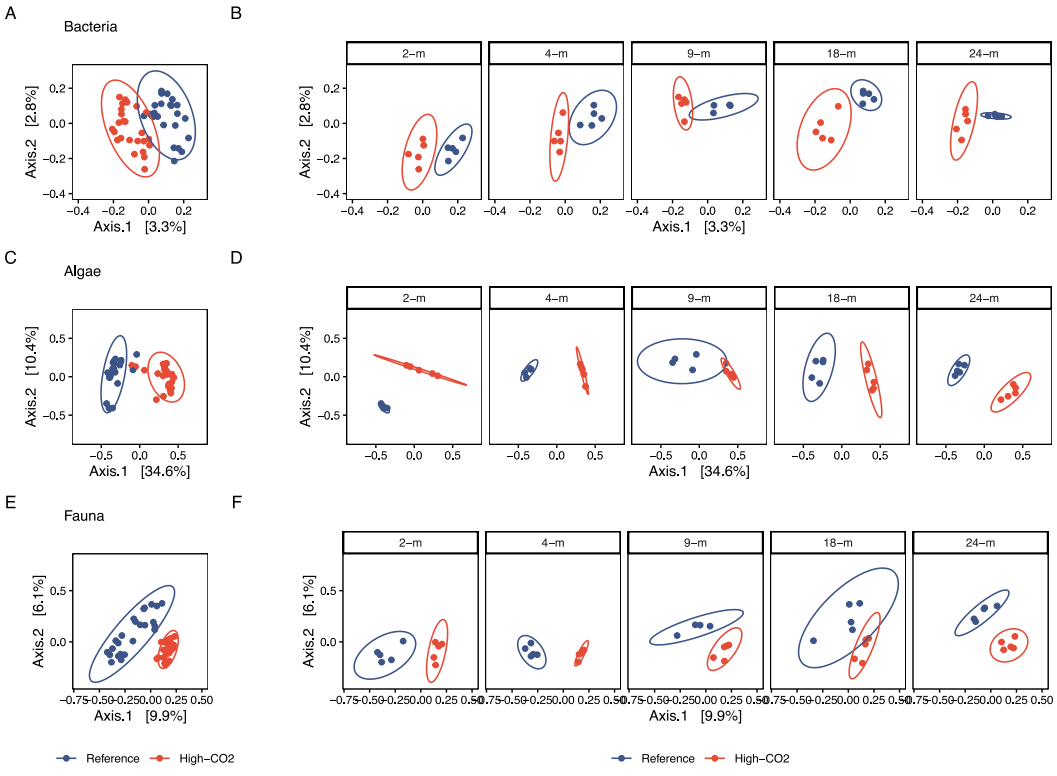

Figure 1: nMDS of community composition based on meta-barcoding between Reference (blue) and High-CO_2 (red) communities. Each point represents a community, with more similar communities closer to each other. Communities are separated as Bacteria by 16S (A-B), Algae by 18S (C-D), and Fauna by COI (E-F). Panels on the right (B, D and F) show the different durations of development before collection (2, 4, 9, 18 and 24 months).

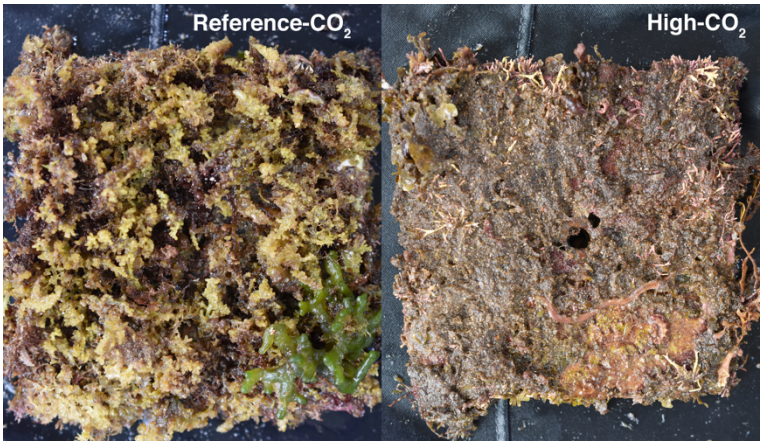

Figure 2: Example photographs from the laboratory of the recruitment tiles after 24-months. Communities on the tiles were visually distinct from each other.

development, which are then locked-in, leaving a species-poor, low complexity community. The simplification of the marine ecosystem, such as by systems shifting to turf dominance, likely leads to functional-biodiversity loss in the system with implications for functioning of the system under future ocean acidification

When assessing the community production rates a clear pattern emerged. Communities within the Reference site consistently demonstrated higher levels of gross primary production (Figure 3A) and community respiration (Figure 3B) compared to the High-CO_2 site. This was driven by the greater biomass, diversity, and complexity of the community. The hindered development of the High-CO_2 community, i.e. the state of being turf-dominated from early to late succession, was also mirrored in the production rates with the rates showing far less change over time (Figure 3A-B).

In conclusion, ocean acidification can set the course of successional development and lead to communities dominated by turf algae, causing reduced algal biomass, diversity and complexity.

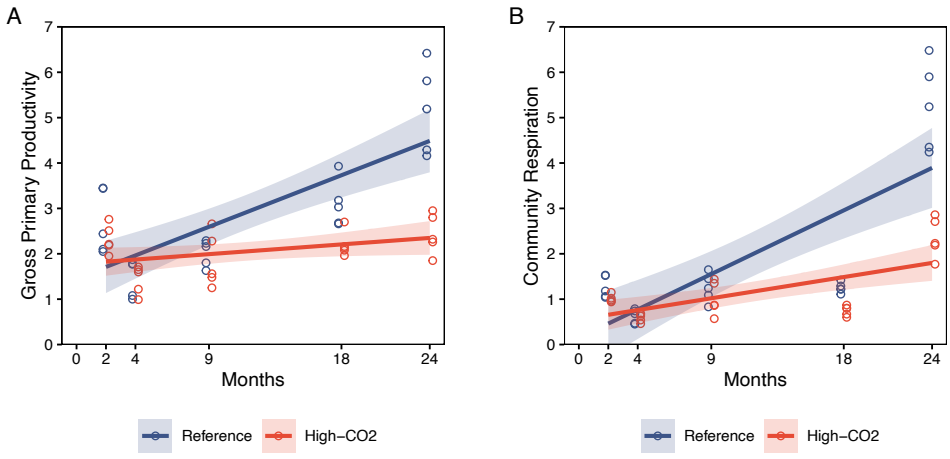

Figure 3: Community production rates of the recruitment tiles for gross primary production (A), and community respiration (B).

５．主な発表論文等

〔雑誌論文〕　計12件（うち査読付論文　12件／うち国際共著　12件／うちオープンアクセス　5件）

１．著者名 Ben P. Harvey, Sylvain Agostini, Koetsu Kon, Shigeki Wada and Jason M. Hall-Spencer	４．巻 11
２．論文標題 Diatoms Dominate and Alter Marine Food-Webs When CO2 Rises	５．発行年 2019年
３．雑誌名 Diversity	６．最初と最後の頁 242
掲載論文のDOI（デジタルオブジェクト識別子） 10.3390/d11120242	査読の有無 有
オープンアクセス オープンアクセスとしている（また、その予定である）	国際共著 該当する

１．著者名 Jason M. Hall-Spencer, Ben P. Harvey	４．巻 3
２．論文標題 Ocean acidification impacts on coastal ecosystem services due to habitat degradation	５．発行年 2019年
３．雑誌名 Emerging Topics in Life Sciences	６．最初と最後の頁 197-206
掲載論文のDOI（デジタルオブジェクト識別子） 10.1042/ETLS20180117	査読の有無 有
オープンアクセス オープンアクセスとしている（また、その予定である）	国際共著 該当する

１．著者名 Hirosuke Hirano, Koetsu Kon, Masa-aki Yoshida, Ben P. Harvey, Davin H. E. Setiamarga	４．巻 58
２．論文標題 The influence of CO2 seeps to coastal environments of Shikine Island in Japan as indicated by geochemistry analyses of seafloor sediments	５．発行年 2019年
３．雑誌名 International Journal of GEOMATE	６．最初と最後の頁 82-89
掲載論文のDOI（デジタルオブジェクト識別子） 10.21660/2019.58.8163	査読の有無 有
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 該当する

１．著者名 Sylvain Agostini, Ben P. Harvey, Shigeki Wada, Koetsu Kon, Marco Milazzo, Kazuo Inaba & Jason M. Hall-Spencer	４．巻 8
２．論文標題 Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical−temperate transition zone	５．発行年 2018年
３．雑誌名 Scientific Reports	６．最初と最後の頁 11354
掲載論文のDOI（デジタルオブジェクト識別子） 10.1038/s41598-018-29251-7	査読の有無 有
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1．著者名 Susan C. Fitzer, Vera Bin San Chan, Yuan Meng, Kanmani Chandra Rajan, Michio Suzuki, Christelle Not, Takashi Toyofuku, Laura Falkenberg, Maria Byrne, Ben P. Harvey, Pierre de Wit, Maggie Cusack, Kunshan Gao, Paul Taylor, Sam Dupont, Jason Hall-Spencer, Vengatesen Thiyagarajan	4．巻 57
2．論文標題 Established and Emerging Techniques for Characterising the Formation, Structure and Performance of Calcified Structures Under Ocean Acidification	5．発行年 2019年
3．雑誌名 Oceanography and Marine Biology: An Annual Review	6．最初と最後の頁 57-94
掲載論文のDOI（デジタルオブジェクト識別子） なし	査読の有無 有
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 該当する

1．著者名 Harvey Ben P.、Kon Koetsu、Agostini Sylvain、Wada Shigeki、Hall‐Spencer Jason M.	4．巻 27
2．論文標題 Ocean acidification locks algal communities in a species‐poor early successional stage	5．発行年 2021年
3．雑誌名 Global Change Biology	6．最初と最後の頁 2174-2187
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1．著者名 Harvey Ben P.、Allen Ro、Agostini Sylvain、Hoffmann Linn J.、Kon Koetsu、Summerfield Tina C.、Wada Shigeki、Hall-Spencer Jason M.	4．巻 4
2．論文標題 Feedback mechanisms stabilise degraded turf algal systems at a CO2 seep site	5．発行年 2021年
3．雑誌名 Communications Biology	6．最初と最後の頁 219
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1．著者名 Wada Shigeki、Agostini Sylvain、Harvey Ben P.、Omori Yuko、Hall-Spencer Jason M.	4．巻 250
2．論文標題 Ocean acidification increases phytobenthic carbon fixation and export in a warm-temperate system	5．発行年 2021年
3．雑誌名 Estuarine, Coastal and Shelf Science	6．最初と最後の頁 107113～107113
掲載論文のDOI（デジタルオブジェクト識別子） 10.1016/j.ecss.2020.107113	査読の有無 有
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1．著者名 Agostini Sylvain、Houlbreque Fanny、Biscere Tom、Harvey Ben P.、Heitzman Joshua M.、Takimoto Risa、Yamazaki Wataru、Milazzo Marco、Rodolfo-Metalpa Riccardo	4．巻 7
2．論文標題 Greater Mitochondrial Energy Production Provides Resistance to Ocean Acidification in “Winning” Hermatypic Corals	5．発行年 2021年
3．雑誌名 Frontiers in Marine Science	6．最初と最後の頁 1235
掲載論文のDOI（デジタルオブジェクト識別子） 10.3389/fmars.2020.600836	査読の有無 有
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1．著者名 Harvey Ben P.、Kerfahi Dorsaf、Jung YeonGyun、Shin Jae-Ho、Adams Jonathan M.、Hall-Spencer Jason M.	4．巻 161
2．論文標題 Ocean acidification alters bacterial communities on marine plastic debris	5．発行年 2020年
3．雑誌名 Marine Pollution Bulletin	6．最初と最後の頁 111749～111749
掲載論文のDOI（デジタルオブジェクト識別子） 10.1016/j.marpolbul.2020.111749	査読の有無 有
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1．著者名 Cattano Carlo、Agostini Sylvain、Harvey Ben P.、Wada Shigeki、Quattrocchi Federico、Turco Gabriele、Inaba Kazuo、Hall-Spencer Jason M.、Milazzo Marco	4．巻 725
2．論文標題 Changes in fish communities due to benthic habitat shifts under ocean acidification conditions	5．発行年 2020年
3．雑誌名 Science of The Total Environment	6．最初と最後の頁 138501～138501
掲載論文のDOI（デジタルオブジェクト識別子） 10.1016/j.scitotenv.2020.138501	査読の有無 有
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 該当する

1．著者名 Kerfahi Dorsaf、Harvey Ben P.、Agostini Sylvain、Kon Koetsu、Huang Ruiping、Adams Jonathan M.、Hall-Spencer Jason M.	4．巻 22
2．論文標題 Responses of Intertidal Bacterial Biofilm Communities to Increasing pCO2	5．発行年 2020年
3．雑誌名 Marine Biotechnology	6．最初と最後の頁 727～738
掲載論文のDOI（デジタルオブジェクト識別子） 10.1007/s10126-020-09958-3	査読の有無 有
オープンアクセス オープンアクセスではない、又はオープンアクセスが困難	国際共著 該当する

〔学会発表〕　計3件（うち招待講演　1件／うち国際学会　3件）

1．発表者名 Harvey, B.P.; Agostini, S.; Allen, R.; Hall-Spencer, J.M.
2．発表標題 Turf algae dominance under ocean acidification - are positive feedback mechanisms locking this degraded system in place?
3．学会等名 The 12th Meeting of the International Temperate Reefs Symposium（国際学会）
4．発表年 2019年

1．発表者名 Ben Harvey
2．発表標題 Ecosystem effects of ocean acidification
3．学会等名 JPGU-AGU（招待講演）（国際学会）
4．発表年 2017年

1．発表者名 1.Harvey B.P., Allen R., Agostini S., Hoffmann L.J., Kon K., Summerfield T.C., Wada S., and Hall-Spencer J.M.
2．発表標題 The dominance of turf-forming diatoms under ocean acidification and their role in community succession
3．学会等名 Marine Biotechnology Conference 2019（国際学会）
4．発表年 2019年

〔図書〕　計0件

〔産業財産権〕

〔その他〕

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6．研究組織

	氏名 （ローマ字氏名） （研究者番号）	所属研究機関・部局・職 （機関番号）	備考

7．科研費を使用して開催した国際研究集会

〔国際研究集会〕　計0件

８．本研究に関連して実施した国際共同研究の実施状況

共同研究相手国	相手方研究機関