BRIEF COMMUNICATION

THE IMPACTS OF PAST CLIMATE CHANGE ON SUB-ANTARCTIC NEARSHORE ECOSYSTEMS

by Ceridwen I. Fraser

(with one text-figure and two plates)

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Pleistocene glacial–interglacial cycles would have resulted in drastic changes in the structure of sub-Antarctic littoral ecosystems. Genetic data indicate that the large kelps that dominate intertidal and shallow subtidal sub-Antarctic shores today (such as *Macrocystis pyrifera* and *Durvillaea antarctica*) were extirpated from these high latitude regions by sea ice scour during glacial maxima. These macroalgae, and their associated faunal communities, were able to return to the sub-Antarctic islands during interglacial periods by drifting at sea in the path of the Antarctic Circumpolar Current. During glacial maxima, sub-Antarctic littoral communities would have been severely reduced, comprising mainly ice-scour hardy taxa such as small and/or seasonal macroalgae, and mobile molluscs.

Key Words: sub-Antarctic, ice scour, postglacial recolonisation, rafting, West Wind Drift, global warming.

INTRODUCTION

Earth's climate fluctuated between glacial and interglacial periods throughout the Quaternary (Petit *et al.* 1999). With each major climate shift, many organisms were forced to change their distributional ranges, generally moving towards the equator as the planet entered an ice age, and towards the poles during interglacial periods (e.g., Hewitt 2000, Fraser *et al.* 2012). Where organisms have recolonised higher-latitude regions post-glacially, these more recently established populations generally show lower genetic diversity than at lower latitudes, where populations have been able to persist locally or *in situ* for longer periods (Hewitt 2000).

Several recent studies on Southern Hemisphere sub-polar and cool-temperate littoral ecosystems have found such latitudinal genetic diversity gradients, indicating that many of the sub-Antarctic islands have been recolonised post-glacially (approximately during the last 18 000 years) by highly-dispersive marine species that are unable to withstand ice scour (Fraser *et al.* 2009, Nikula *et al.* 2010). In contrast, sub-Antarctic marine species that are less adversely affected by sea ice do not appear to show strong genetic diversity gradients. These biological studies support the hypothesis that Antarctic sea ice extended to most of the sub-Antarctic islands at the Last Glacial Maximum (LGM) (Fraser *et al.* 2009) (fig. 1). Furthermore, they suggest that the ecological structure of contemporary sub-Antarctic littoral ecosystems is relatively young, and has changed drastically throughout the glacial–interglacial cycles of the Quaternary.

SUB-ANTARCTIC LITTORAL ECOSYSTEMS TODAY

Many intertidal and shallow subtidal ecosystems of the sub-Antarctic islands north of the Antarctic Polar Front (APF) are dominated by Southern Bull-Kelp (*Durvillaea antarctica* (Chamisso) Hariot) communities (e.g., Klemm & Hallam 1988) (pl. 1). Southern Bull-Kelp can reach densities of more than 100 kg wet mass/m^2 (Haxen & Grindley 1985), and makes a large contribution to local marine (Kaehler *et al.* 2000) and terrestrial (Dufour 2011) trophic webs. Kelp plays an important role in local community structure by facilitating settlement and growth of some macroalgal species over others (Taylor & Schiel 2005), and providing habitat and food for a diverse array of invertebrate taxa (Edgar & Burton 2000, Smith & Simpson 2002) including polychaetes, echinoderms, crustaceans and molluscs. Beach-cast bull-kelp (wrack) is consumed by a wide variety of insects and crustaceans (Dufour 2011) which in turn form the prey of many birds.

In deeper (>5m) subtidal sub-Antarctic waters, the giant kelp *Macrocystis pyrifera* (Linnaeus) C.Agardh dominates and, like *D. antarctica*, performs important ecosystem-structuring services by providing habitat and food for many organisms. Pugh & Davenport (1997) hypothesised that *M. pyrifera* might survive some degree of ice scour as its holdfasts attach to the substrate deeply enough to avoid the ice foot. Molecular data, however, indicate that this species has probably recolonised many sub-Antarctic islands post-glacially (Macaya & Zuccarello 2010b), suggesting it does not survive long periods of sustained ice scour. Indeed, *Macrocystis* is not presently recorded from any of the islands within the northern limit of sea ice. More than a century ago, Skottsberg (1904) noted the absence of *Macrocystis* from the South Orkney Islands and suggested it was unlikely to occur near any islands within the northern limit of drifting sea ice (which he defined as the "Antarctic" zone).

Molecular studies of *D. antarctica* (Fraser *et al.* 2009), *M. pyrifera* (Macaya & Zuccarello 2010b), and some kelp-associated invertebrates (Nikula *et al.* 2010) indicate that most sub-Antarctic kelp communities have recolonised LGM sea ice-affected regions (fig. 1) post-glacially, presumably via rafting. Circumpolar dispersal would have been facilitated by the strong eastward-flowing Antarctic Circumpolar Current (ACC), also known as the West Wind Drift (Waters 2008). Tens of millions of detached *D. antarctica* are estimated to be drifting in the path of the ACC at any time (Smith 2002), and can carry associated invertebrate communities

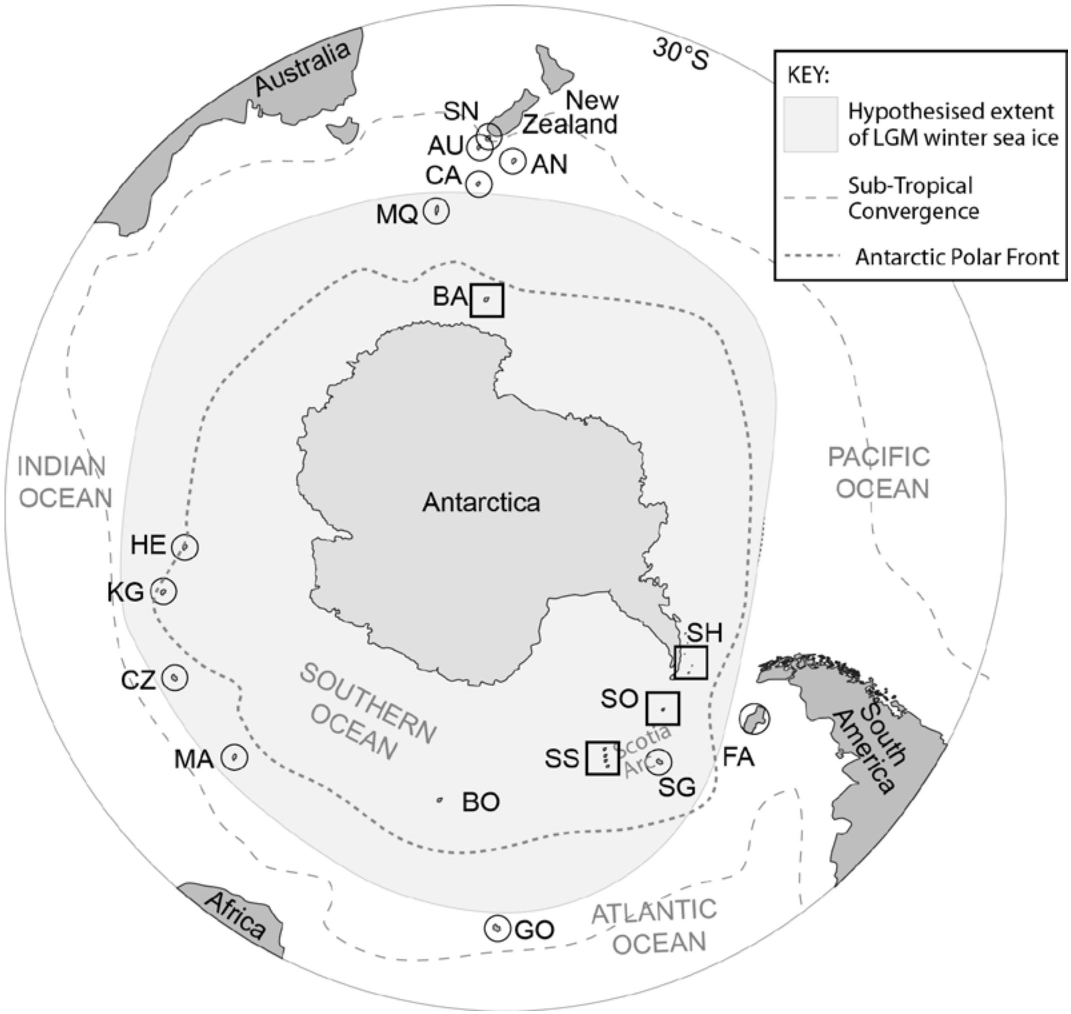

FIG. 1 — Map showing the locations of major sub-Antarctic and some Antarctic islands, with those indicated by circles not currently within the extent of Antarctic sea ice, and those indicated by squares within winter sea ice range. AN: Antipodes Islands; AU: Auckland Islands; BA: Balleny Island; BO: Bouvet Island; CA: Campbell Island; CZ: Crozet Islands; FA: Falkland Islands (also known as Malvinas); GO: Gough Island; HE: Heard Island; KG: Kerguelen Islands; MA: Marion and Prince Edward Islands; MQ: Macquarie Island; SG: South Georgia; SN: Snares Islands; SO: South Orkney Islands; SS: South Sandwich Islands; SH: South Shetland Islands. Note: not all islands within the region are shown.

long distances among isolated oceanic landmasses (Fraser *et al.* 2011). Post-glacial recolonisation of the sub-Antarctic by rafting would therefore have been possible even for some otherwise sedentary or poorly motile organisms. Based on molecular patterns, recolonisation by *D. antarctica* is inferred to have occurred from a refugium in the New Zealand sub-Antarctic (Fraser *et al.* 2009, Fraser *et al.* 2010a).

Not all intertidal and shallow subtidal organisms are likely to have been driven locally extinct at sub-Antarctic islands within the range of sea ice at the LGM. Some taxa are ice-resistant, able to survive at depths below the reach of scouring ice, or in shelters such as rock cracks (Barnes 1999), and these might have survived Quaternary ice ages *in situ* on the islands (Fraser *et al.* 2012). Thus, sub-Antarctic nearshore ecosystems could have cycled, with glacial–interglacial changes, between ecosystems structured largely by the ice-scour susceptible kelps *D. antarctica* and *M. pyrifera*, and more ice-resilient communities.

SUB-ANTARCTIC LITTORAL ECOSYSTEMS DURING GLACIAL MAXIMA

During Quaternary glacial maxima, when Antarctic sea ice is hypothesised to have – at least occasionally – extended far enough north to have affected Marion, Macquarie, Crozet, Kerguelen and Heard islands (Fraser *et al.* 2009, Fraser *et al.* 2012) (fig. 1), sub-Antarctic intertidal and shallow subtidal ecosystems might have been comparable to those found today at islands still within the reach of Antarctic winter sea ice, such as the South Shetland or South Orkney islands (pl. 2). There, sparse and relatively small macroalgae with short or biphasic/seasonal life cycles dominate the shallow marine floral assemblages, and hardy, motile invertebrates such as limpets and amphipods can persist despite frequent scouring of the rocky shores by ice. Mercier & Hamel (2005, p. 87) described the littoral flora and fauna of the Scotia Arc islands:

PLATE 1

Durvillaea antarctica *is an important ecosystem-structuring species in the sub-Antarctic. These photographs, from Marion Island in April 2007, show: (A)* D. antarctica *growing densely in the intertidal, as well as detached and cast up on the beach (Fur and Elephant seals indicate scale), and (B)* D. antarctica *and other macroalgae covering almost all available rocky substrate in the intertidal (scale represents approximately 20 cm) (Photos: Ceridwen Fraser).*

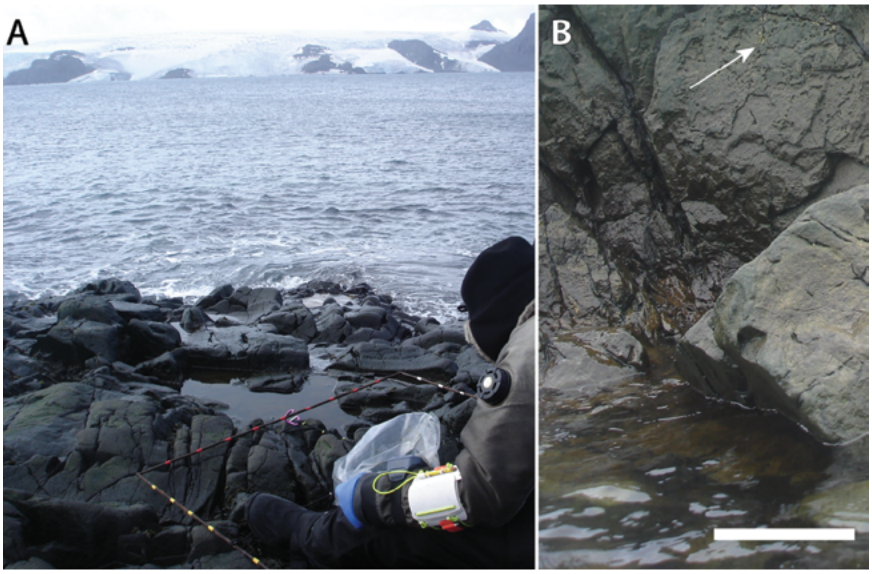

PLATE 2

At the peak of the last Ice Age, many sub-Antarctic littoral ecosystems probably resembled those of Antarctic islands currently within the reach of sea ice, such as the South Shetland Islands. These photographs, taken during intertidal surveys in the South Shetland Islands (King George Island) in February 2008, show ice-scoured rocky shores lacking the diverse macroalgal cover of sub-Antarctic islands. Some algae (see arrow in panel B) and motile fauna such as limpets can persist by sheltering in rock cracks and crevices. Scale in panel B represents approximately 40 cm (Photos: A: Carlos Olavarria; B: Emma Newcombe).

> *Overall, the biota of the intertidal region is poor... the midlittoral zone … is characterized by the presence of the* Porphyra *algae … there are also algae in the tide pools and crevices. Limpets … occur in crevices, whereas amphipods, nemertines, and flatworms are found clustered under stones and rocks. The tide pools of the midlittoral are home to many Antarctic species of algae such as* Leptosomia, Iridaea, Adenocystis *that can also extend their distribution to the infralittoral fringe area with* Desmarestia, Curdiea, Monostroma, *and* Plocamium. *The infralittoral fringe is characterized by numerous algae, mainly of the genera* Desmarestia *and* Ascosiera. *The huge* Phyllogigas grandifolius [now *Himantothallus grandifolius*] *dominates this* [subtidal] *area …*

On South Georgia, some littoral regions are scoured by ice breaking away from the island's glaciers, whereas other areas are rarely impacted by ice, providing an interesting system for studies of the impacts of ice scour. An ecological study on South Georgia by Pugh & Davenport (1997) documented differences in these shallow marine ecosystems, and demonstrated that some macroalgae, such as *Porphyra* and *Urospora* species, survive in rock crevices in the ice scoured areas.

Many of the intertidal/shallow subtidal algae (e.g., *Desmarestia ligulata* (Stackhouse) J.V.Lamouroux, *Adenocystis utricularis* (Bory de Saint-Vincent) Skottsberg, *Bostrychia intricata* (Bory de Saint-Vincent) Montagne, several *Porphyra* species) of islands presently within Antarctic sea ice extent also occur on sub-Antarctic islands further north. Preliminary molecular data from *A. utricularis* and *B. intricata* – circumpolar macroalgae that occur throughout the sub-Antarctic, including on some currently ice-affected islands – indicate that these taxa do not show classic genetic signatures of post-glacial recolonisation of LGM ice-affected islands (Fraser, unpublished data). These species may therefore have persisted *in situ* throughout recent glacial maxima. Similarly, limpets of the genus *Nacella* show considerable phylogeographic diversity in the sub-Antarctic (González-Wevar *et al.* 2010), indicating that congeners have likely been scattered throughout the sub-Antarctic since well before the LGM. Sub-Antarctic littoral ecosystems during glacial periods therefore probably comprised a depauperate subset of modern-day sub-Antarctic taxa.

CONCLUSIONS AND IMPLICATIONS

Some of the dominant macroalgal species – and associated invertebrate communities – of the littoral ecosystems of many sub-Antarctic islands today were apparently extirpated from the islands during the last Ice Age (and presumably at previous Quaternary glacial maxima). When sea ice extended far enough north to scour sub-Antarctic shores, littoral ecosystems would have been drastically different, with diversity reduced to those species capable of surviving in ice-affected regions. Dispersal by rafting would have allowed recolonisation of the islands by ice-sensitive taxa during warmer interglacial periods.

Sub-Antarctic littoral ecosystems thus appear to have been able to recover from some of the impacts to biodiversity of Quaternary climate change cycles, but predicting the impacts of, and biological response to, future climate change in the region is not straightforward. Global average temperatures in coming decades are predicted to exceed any experienced during the Quaternary (I.P.C.C. 2007), and using pre-Quaternary warm periods as analogues of future climate change is complicated by uncertainties related to factors such as changes in oceanography, topography and continental positions (Haywood *et al.* 2011). Global warming is expected to lead to poleward range shifts for many taxa (Hickling *et al.* 2006), but southward dispersal of sub-Antarctic taxa would require traversal of oceanic barriers such as the Antarctic Polar Front (Fraser *et al.* 2012).

Fortunately, the sub-Antarctic is expected to experience slower rates of global warming than at similar latitudes in the Northern Hemisphere (Sandel *et al.* 2011), perhaps largely due to oceanic climate buffering. *D. antarctica* cannot tolerate high water temperatures (greater than about 17°C), and its northern limit is currently approximately in line with the limit of sub-Antarctic waters (although relatively sparse northern populations occur up to about 30–35°S in the cool-temperate waters of New Zealand and Chile) (Fraser *et al.* 2010b). The now monospecific genus *Macrocystis* has a slightly broader distribution in the Southern Hemisphere, ranging from the sub-Antarctic to cool-temperate latitudes (e.g., the southern coast of South Africa, southeastern Australia, and along the path of the Humboldt Current in South America) (Macaya & Zuccarello 2010a). If either species is extirpated from sub-Antarctic islands by warming ocean temperatures, significant changes to littoral (and, indirectly, terrestrial) ecosystems in the region are sure to result, but these changes will be unlike any the region has experienced during the past 2–3 million years.

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REFERENCES

Barnes, D.K.A. 1999: The influence of ice on polar nearshore benthos. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 401–407.

Dufour, C. 2011: The influence of stranded kelp (*Durvillaea antarctica*) on the macrofaunal assemblages of a southern New Zealand exposed sandy beach. Unpubl. MSc thesis, University of Otago, Dunedin: 98. http://hal.handle.net/10523/1940

Edgar, G.J. & Burton, H.R. 2000: The biogeography of shallow-water macrofauna at Heard Island. *Papers and Proceedings of the Royal Society of Tasmania*, **133**: 23–26.

Fraser, C., Thiel, M., Spencer, H. & Waters, J. 2010a: Contemporary habitat discontinuity and historic glacial ice drive genetic divergence in Chilean kelp. *BMC Evolutionary Biology*, **10**: 203.

Fraser, C.I., Nikula, R., Ruzzante, D.E. & Waters, J.M. 2012: Poleward bound: biological impacts of Southern Hemisphere glaciation. *Trends in Ecology & Evolution* **27**: 462–471.

Fraser, C.I., Nikula, R., Spencer, H.G. & Waters, J.M. 2009: Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. *Proceedings of the National Academy of Sciences, USA* **106**: 3249–3253.

Fraser, C.I., Nikula, R. & Waters, J.M. 2011: Oceanic rafting by a coastal community. *Proceedings of the Royal Society B: Biological Sciences* **278**: 649–655.

Fraser, C.I., Winter, D.J., Spencer, H.G. & Waters, J.M. 2010b: Multigene phylogeny of the southern bull-kelp genus *Durvillaea* (Phaeophyceae: Fucales). *Molecular Phylogenetics and Evolution* **57**: 1301–1311.

González-Wevar, C.A., Nakano, T., Canete, J.I. & Poulin, E. 2010: Molecular phylogeny and historical biogeography of *Nacella* (Patellogastropoda: Nacellidae) in the Southern Ocean. *Molecular Phylogenetics and Evolution* **56**: 115–124.

Haxen, P.G. & Grindley, J.R. 1985: *Durvillaea antarctica* production in relation to nutrient cycling at Marion Island. *In* Siegfried,W.R., Condy, P.R.& Laws, R.M. (eds): *Antarctic Nutrient Cycles and Food Webs.* Springer-Verlag, Berlin: 637–640.

Haywood, A.M., Ridgwell, A., Lunt, D.J., Hill, D.J., Pound, M.J., Dowsett, H.J., Dolan, A.M., Francis, J.E. & Williams, M. 2011: Are there pre-Quaternary geological analogues for a future greenhouse warming? *Philosophical Transactions of the Royal Society A: Mathematical, Physical*

and Engineering Sciences **369**: 933–956.
Hewitt, G. 2000: The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907–913.
Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. 2006: The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**: 450–455.
I.P.C.C. 2007: *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007*. Cambridge University Press, Cambridge, UK: 976 pp.
Kaehler, S., Pakhomov, E.A. & Mcquaid, C.D. 2000: Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by d13C and d15N analysis. *Marine Ecology Progress Series* **208**: 13–20.
Klemm, M.F. & Hallam, N.D. 1988: Standing crop of *Durvillaea antarctica* (Chamisso) Hariot (Phaeophyta) on the Australian sub-Antarctic Macquarie and Heard Islands. *Phycologia* **27**: 505–509.
Macaya, E.C. & Zuccarello, G.C. 2010a: DNA barcoding and genetic divergence in the Giant Kelp *Macrocystis* (Laminariales). *Journal of Phycology* **46**: 736–742.
Macaya, E.C. & Zuccarello, G.C. 2010b: Genetic structure of the giant kelp *Macrocystis pyrifera* along the southeastern Pacific. *Marine Ecology-Progress Series* **420**: 103–112.
Mercier, A. & Hamel, J.-F. 2005: Atlantic Ocean islands, coastal ecology. *In* Schwartz, M.L. (ed.): *Encyclopedia Of Coastal Science*. Springer, Dordrecht: 84–88.
Nikula, R., Fraser, C.I., Spencer, H.G. & Waters, J.M. 2010: Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology-Progress Series* **405**: 221–230.
Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N., Barnola, J., Basile, I., Bender, M., Chappellaz, J. & Delaygue, G. 1999: Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429–436.
Pugh, P.J.A. & Davenport, J. 1997: Colonisation vs. disturbance: The effects of sustained ice-scouring on intertidal communities. *Journal of Experimental Marine Biology and Ecology* **210**: 1–21.
Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. 2011: The influence of late Quaternary climate-change velocity on species endemism. *Science* **334**: 660–664.
Skottsberg, C. 1904: On the zonal distribution of South Atlantic and Antarctic vegetation. *The Geographical Journal* **24**: 655–663.
Smith, S.D.A. 2002: Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography* **11**: 67–69.
Smith, S.D.A. & Simpson, R.D. 2002: Spatial variation in the community structure of intertidal habitats at Macquarie Island (sub-Antarctic). *Antarctic Science* **14**: 374–384.
Taylor, D.I. & Schiel, D.R. 2005: Self-replacement and community modification by the southern bull kelp *Durvillaea antarctica*. *Marine Ecology-Progress Series* **288**: 87–102.
Waters, J.M. 2008: Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography* **35**: 417–427.

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