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**Are oceanic fronts ecotones? Seasonal changes along the Subtropical Front show
fronts as bacterioplankton transition zones but not diversity hotspots**

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1 **Ecotones are regarded as diversity hotspots in terrestrial systems, but it is**
2 **unknown if this “ecotone effect” occurs in the marine environment. Oceanic**
3 **fronts are widespread mesoscale features, present in the boundary between**
4 **different water masses, and are arguably the best potential examples of ecotones**
5 **in the ocean. Here we performed the first seasonal study along an oceanic front,**
6 **combining 16S rRNA gene sequencing coupled with a high spatial resolution**
7 **analysis of the physical properties of the water masses. Using the Subtropical**
8 **Frontal Zone off New Zealand we demonstrate that fronts delimit shifts in**
9 **bacterioplankton community composition between water masses, but that the**
10 **strength of this effect is seasonally dependent. While creating a transition zone**
11 **where physicochemical parameters and bacterioplankton communities get**
12 **mixed, this ecotone does not result in increased diversity. Thus unlike terrestrial**
13 **ecotones, oceanic ecotones like fronts are boundaries but not hotspot of**
14 **bacterioplankton diversity in the ocean.**

15

16 Ecotones are boundaries, or transition zones, between ecological communities,
17 ecosystems, or ecological regions usually formed by steep environmental gradients
18 (Kark 2013). In terrestrial systems, species richness, abundances and productivity
19 tend to peak in ecotones (Kark 2013, Smith et al 1997). However, the study of
20 ecotones and its effects in the open ocean environment has not received the same
21 attention as in terrestrial systems, probably because transition zones are not as easy to
22 detect as in land. The best example of ecotones in the marine environment is oceanic
23 fronts. Fronts are areas where distinct water masses meet creating enhanced horizontal
24 gradients of physicochemical properties (e.g. temperature, salinity) (Belkin 2003).
25 Fronts are widespread and linked to large effects on marine ecosystems (Le Fevre

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26 1987, Longhurst 2006), including increased phytoplankton diversity (Barton et al
27 2010, Ribalet et al 2010) and productivity (Belkin et al 2009, Okkonen et al 2004,
28 Springer et al 1996), yet their role in demarking bacterioplankton (i.e., defined as
29 bacteria and archaea) communities shifts is unclear. This is critical since heterotrophic
30 bacterioplankton make up the largest living biomass in the ocean, and drive oceanic
31 biogeochemical cycles, regulating the composition of Earth's atmosphere and
32 influencing climate (Buchan et al 2014, Kirchman 2010). Prior work revealed oceanic
33 fronts can act as ecotones, creating boundaries for bacterioplankton distribution in the
34 ocean (Baltar et al 2016a). However, limited sampling and strong seasonal variability
35 prevented testing of whether the front acted as a bacterioplankton diversity hotspot.

36 Here we performed the first seasonal high spatial resolution transect study of
37 bacterioplankton diversity across an oceanic front (the Subtropical Frontal Zone off
38 New Zealand). This study involved 6 sampling cruises from January 2014 to April
39 2015. We combined a high-resolution characterization of the front (via a continuous
40 temperature and salinity recorder) and the analysis of bacterioplankton diversity
41 (based on 16S rRNA gene Illumina sequencing (see Supplementary Information)). In
42 all the cruises, bacterioplankton diversity and chlorophyll-a concentration was
43 sampled at eight surface (2 m) water stations along the 48 km long transect, following
44 the same approach as in previous studies (Baltar et al 2015, Baltar et al 2016a). The
45 Subtropical Front is where the warm and salty subtropical waters (STW) and the cold,
46 high-nutrient low-chlorophyll sub-Antarctic waters (SAW) meet. This front is
47 constrained along the SE continental shelf of New Zealand to about 40-50 km
48 offshore, compacting the frontal zone to a width of 2-10 km (Heath 1972).

49 Temperature and salinity changes along the transect retained the same structure

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50 throughout the study, with the presence of the 3 main water masses located in this
51 area (Fig. 1A). Off the coast, the low salinity neritic waters (NW; characterized by
52 riverine inputs) encounter and gradually mix with the warmer and saltier subtropical
53 waters (STW). This is followed by a sharp (taking place in < 2 km between stations 3
54 and 5) drop in temperature and salinity, demarking the front and the convergence of
55 the STW with the offshore SAW. As previously reported in other studies across this
56 transect (Jillett, 1969; Heath, 1972; Shaw and Vennell, 2001; Hopkins et al., 2010),
57 the location, width and strength of the front oscillates seasonally (Fig. 1B) (Heath
58 1972, Hopkins et al 2010, Jones et al 2013).

59 A clear water mass dependent seasonal change in phytoplankton biomass
60 (chlorophyll-a) was observed along the transect (Fig. 2A). These blooms within the
61 STW coincided with the transition from the Austral winter (June-July 2014) to the
62 spring-summer seasons, as well as a smaller autumnal bloom. Observed chlorophyll-a
63 concentrations reached $>4 \text{ mg m}^{-3}$ in December 2014 and $>2 \text{ mg m}^{-3}$ in April 2015
64 during the study, in agreement with previous studies where the threshold of $>1 \text{ mg m}^{-3}$
65 indicated bloom conditions (Hopkins et al 2010, Jones et al 2013). While strong
66 seasonality in phytoplankton biomass was detected in the STW, changes in the NW
67 and front were less pronounced, and absent within the SAW. This is consistent with
68 the characteristic iron-limited primary production of the high-nutrient low-chlorophyll
69 SAW (Baltar et al 2015, Jones et al 2013, Sander et al 2014). However, chlorophyll-a
70 concentrations were not higher within the frontal waters at any time point, with
71 values intermediate to those in STW and SAW, reflecting the mixing nature of fronts.

72 Changes in chlorophyll-a concentration were negatively correlated ($p < 0.01$) to
73 bacterioplankton diversity (based on the Shannon Index), with fluctuations across the

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74 transect modified by seasons (Fig2 B-D, and Tables S1-2). Changes in Shannon
75 diversity were strongest across time (ANOVA F Ratio = 51.60, p value <.0001), with
76 no significant effect across the water masses (p = 0.45) unless time was accounted for
77 (water mass x time: F Ratio = 5.13, p value <.0001). While changes in
78 bacterioplankton richness were observed and mirrored trends in diversity, it suggests
79 that community structure (changes in evenness) where the strongest factor. Maximum
80 diversity occurred during winter (June and July 2014) and the lowest in summer
81 (December 2014). This inverse relationship between bacterioplankton diversity and
82 phytoplankton biomass is consistent with the common negative diversity–productivity
83 relationship found in aquatic ecosystems (Baltar et al 2016b, Smith 2007). This is
84 specifically pronounced in areas with larger blooms (STW and the frontal waters)
85 (Fig. 2D), which are the water masses with the strongest seasonal variations in
86 chlorophyll-a and bacterioplankton diversity. Consistent with observations for
87 phytoplankton biomass, bacterioplankton diversity did not peak in the front, with
88 diversity values intermediate to those for SAW and STW.

89 Our results demonstrate that while fronts serve as ecotones in the sense of
90 delimiting the distribution of bacterioplankton, their strength is not constant, but
91 seasonally driven. This seasonality is linked to differences in phytoplankton biomass
92 across the different water masses (e.g. December 2014). While oceanic fronts are
93 clear boundaries, we demonstrate that they are not bacterioplankton diversity hotspots
94 in contrast to observations for terrestrial plants. This might be due to the more
95 dynamic nature of oceanic fronts, that experience continuous mixing, enlarging and
96 contracting events resulting in a less stable environment than terrestrial ecotones.

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99 **Conflict of interest**

100 The authors declare no conflict of interest.

101

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107 Supplementary information is available at The ISME Journal's website' at the end of
108 the article and before the references.

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180 **Figure legends**

181 **Figure 1. (A)** Physicochemical changes in salinity (dashed) and temperature (solid)
182 along the surface waters of the transect in April 2015, as a representation of the
183 general structure of the water masses encountered in study region. The stations are
184 shown as vertical lines, with their predicted water masses given by colour. Salmon
185 pink = Neritic Water (NW), Green = Subtropical Water (STW), Blue = Frontal Water,
186 Purple = Sub-Antarctic Water (SAW). This is an example of how the water masses
187 were in April 2015, but their location shift throughout the study. **(B)** Summary of how
188 the water masses shifted throughout the duration of the study, with sampling locations
189 shown in black.

190

191 **Figure 2. (A)** Chlorophyll-a concentration, and **(B)** bacterioplankton diversity
192 (Shannon index) in the surface waters along the transect in the six cruises performed
193 from January 2014 to April 2015. Different sampling cruises are denoted in different
194 colors, and the symbols denote different water masses. **(C)** Relation between
195 chlorophyll-a concentration and bacterioplankton diversity (Shannon index) with all
196 samples pooled together or **(D)** with samples separated by water mass. Neritic Water
197 (NW), Sub-Antarctic Water (SAW), Subtropical Water (STW), frontal zone
198 (FRONT).



