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# Fluctuations in Adélie penguin prey size in the mid to late Holocene, northern Marguerite Bay, Antarctic Peninsula

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**Abstract** We investigated temporal changes in Adélie penguin prey size in northern Marguerite Bay, Antarctic Peninsula, through excavations of three abandoned and one active colony at Lagoon (67°35′S, 68°16′W) and Ginger Islands (67°45′S, 68°41′W), respectively, in austral summer 1999/2000. Radiocarbon dates on penguin bones and eggshell fragments collected at each site indicate that Lagoon Island was first occupied after 6000 BP and Ginger Island near 2275 BP. Identifiable non-krill prey remains (otoliths and squid beaks) were recovered from ornithogenic soils at all sites, with Antarctic silverfish (*Pleuragramma antarcticum*) and squid (*Psychroteuthis glacialis*) being the most abundant species represented in the deposits. Estimated mean standard lengths and mantle lengths of these two prey taxa, based on regressions with otolith and beak measurements respectively, indicate that Adélie penguins primarily select these prey within a mean size range of 95–117 mm. Prey size also varied significantly across seven occupation periods from 6000 BP to the present, but did not correlate with climate change.

## Introduction

Ornithogenic (bird-caused) soils formed at penguin colonies in Antarctica retain specific chemical and mineral properties for hundreds to thousands of years after these colonies are abandoned (Ugolini 1972; Tatur and Myrcha 1983, 1984, 1989; Myrcha et al. 1985; Tatur 1989). Preserved organic remains in these soils, besides penguin bones and tissue, include hard parts of prey such as fish bones, otoliths (formed of calcareous aragonite), and chitinous squid beaks; krill does not preserve in the sediments (Emslie et al. 1998; Emslie and McDaniel 2002). Previous studies of abandoned colonies have provided data on historical fluctuations in penguin populations (Baroni and Orombelli 1994; Emslie 1995), as well as past diet (Emslie et al. 1998). However, these studies have not addressed non-krill prey size as a function of climate change.

We sampled ornithogenic soils from three abandoned and one modern Adélie penguin colonies at Lagoon (67°35′S, 68°16′W) and Ginger Islands (67°45′S, 68°41′W), northern Marguerite Bay, in the Antarctic Peninsula, to recover dietary remains preserved in these sediments. Previously, we reported on the occupation history and diet of Adélie penguins in relation to climate change during the mid- to late Holocene, based on data from these sites (Emslie 2001; Emslie and McDaniel 2002). Our results indicated that two major prey taxa, Antarctic silverfish (*Pleuragramma antarcticum*) and squid (*Psychroteuthis glacialis*), fluctuated in abundance in the sediments in accordance with cooling and warming trends in the past. Here, we describe these sites in more detail and apply regression formulas on otolith and squid-beak measurements, to estimate standard length of fish and mantle length of squid in life. In addition, we investigated temporal changes in prey size to determine if this variable also has fluctuated over the past 6,000 years in response to climate change or other factors.

## Materials and methods

### Study area

In January and February 2000, ground surveys were completed at six islands in Ryder Bay (Rothera Point): Anchorage, Lagoon (three islands in a group), Leonie, and Killingbeck (Fig. 1). Also, Ginger Island was surveyed on 1 day when ship access was possible. One modern colony on Ginger Island and three abandoned colonies on the largest and northwest island of the Lagoon Island group were excavated (Fig. 1). Elevations of these sites above mean sea level were measured with a transit and stadia rod. Excavation methods, extraction, identification, and calculation of minimum

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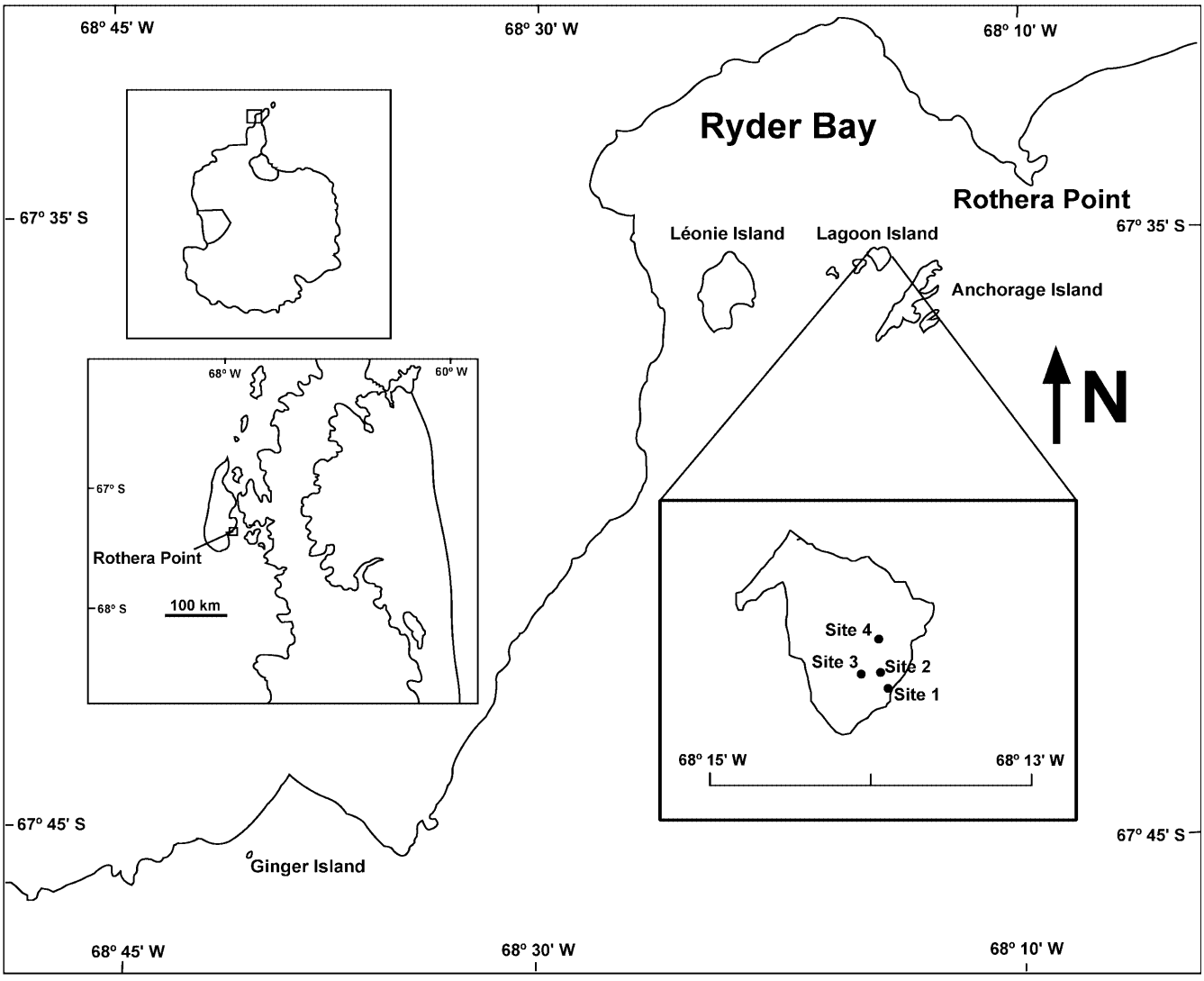


**Fig. 1.** Map of Rothera Point, northern Marguerite Bay, with detail of Ryder Bay and Lagoon Island showing the location of sites 1–4 discussed in the text. An active Adélie penguin colony is located on Ginger Island

number of individuals (MNI) represented by all prey remains from the ornithogenic sediments at these sites are discussed by Emslie and McDaniel (2002).

## Site descriptions

Four sites were located on Lagoon Island. Site 1 consisted of a concentration of surface pebbles on the beach just above high-tide line on the south central side of the island (Fig. 1). The surface was covered with a high concentration of penguin bones, but unlike those that characterize abandoned colonies (Emslie 1995), most of the bones were from adult penguins. A 1×1 m test pit was excavated in five levels in these sediments to a depth of 30 cm. Level 1 (0–10 cm) consisted of loose pebbles and bone with little sediment; the remaining four levels were excavated in 5-cm increments. The number of bones decreased with depth, and few eggshell fragments, which also characterize abandoned colonies, were recovered from the sediments. Given the near absence of juvenile penguin bones and eggshell fragments, along with the abundance of adult bones from this site, it is hypothesized that this area was used only by molting penguins in the past and not as a breeding colony. No radiocarbon dates were obtained on samples from this site.

Site 2 was located on the beach terrace immediately above site 1 (Fig. 1). It consisted of a small pebble concentration, approximately 13 m north-south and 7 m east-west, on level terrain 9 m above sea level. Level 1 consisted of loose pebbles and penguin bones to a depth of 7–13 cm below the surface. Level 2, where sediments first appeared, was excavated to 15 cm. Thereafter, the pit was excavated in 5-cm levels to a depth of 40 cm (levels 3–7). Each level was similar and characterized by pebbles and reddish-brown ornithogenic sediments containing bone and eggshell fragments. A natural gray sand and gravel layer was encountered at 40 cm depth.

Site 3 was located on a higher terrace above and west of site 2 (Fig. 1) at an elevation of 17–18 m. The pebble concentration here measured 20 m north-south and 30 m east-west. Only the surface 2 cm of a 1×1 m test pit placed in the center of this site consisted of loose pebbles, but no bones. Level 2 (2–15 cm) consisted of pebbles and ornithogenic sediments. Subsequent levels below this were excavated in 10-cm increments to a depth of 45 cm (levels 3–5). As with site 2, these levels consisted of reddish-brown ornithogenic soils, pebbles, and eggshell fragments until gray sand, gravel, and bedrock were encountered.

Site 4 was a pebble concentration approximately 10–15 m in diameter, located nearer the center of Lagoon Island on top of a small ridge at approximately 17–18 m in elevation (Fig. 1). A 1×1 m test pit was excavated to a depth of 35 cm. Level 1 consisted

of loose pebbles extending to a depth of 8 cm before reddish-brown ornithogenic soils were encountered. Level 2 was excavated to a depth of 15 cm with subsequent levels (3–4) excavated in 10-cm increments until gray sands and bedrock were reached.

Ginger Island is a small island located approximately 28 km southwest of Lagoon Island (Fig. 1). This island was accessed by ship and has an active Adélie penguin colony, as well as a small colony of blue-eyed shags (*Phalacrocorax atriceps*). A 1×1 m test pit was excavated near the center of the penguin colony after chicks had creched and were no longer occupying nest sites. Compacted sediments and guano composed the first level, which was removed to a depth of 2 cm to expose remaining ornithogenic sediments below. These sediments were excavated in 5-cm levels through level 6. Levels 2 and 3 consisted of dark-brown to black decomposing organic matter, bone, and eggshell fragments, which graded into reddish-brown ornithogenic sediments below. The three lowest levels (7–9), where few bones or other remains were recovered, were excavated in 10-cm increments to a depth of 57 cm, before beach gravels were encountered.

Ornithogenic sediments collected from each site were initially washed through stacked screens with mesh size of 0.64, 0.32, and 0.025 cm. Sediments trapped by the two smaller screens were returned to the laboratory for re-washing and sorting, using a low-power (×5–10) binocular microscope. All test pits were backfilled at the conclusion of the excavations. Occupation history of Adélie penguins in the study area was estimated from 16 radiocarbon dates obtained from bone and eggshell fragments collected at Lagoon Island sites 2, 3, and 4, and from the active colony at Ginger Island (see Emslie 2001; Emslie and McDaniel 2002).

### Quantification of paleodiet

Calcareous otoliths and chitinous squid beaks are resistant to erosion and digestion, and can be measured to estimate the size of the living organism (Clarke 1986; Jobling and Breiby 1986; Gröger et al. 2000). Measurements of otoliths and squid beaks were completed with a Zeiss Stemi SV 6 dissecting microscope and a digital SPOT RT camera attachment (Diagnostics). Digital images (×1.0) of the dietary remains were imported into the Image-Pro Plus software program version 4.1 (Opelco), where the appropriate measurements were completed.

Standard lengths in millimeters (SL) of *Pleuragramma antarcticum* were determined by incorporating otolith width (OW) measurements (Fig. 2) into a linear regression equation determined by Williams and McEldowney (1990), where $SL = 69.21882\ OW + 15.81990$ ($R = 0.906$). The average SL per time period was calculated to determine if prey size varied through time. The lower rostral length in millimeters (LRL) of each squid beak (Clarke 1986) was used to estimate mantle length (ML) with a regression formula determined by Gröger et al. (2000) where $ML = 50.6895\ LRL - 8.6008\ LRL^2 + 1.0823\ LRL^3 - 8.07019$ ($R^2 = 0.9259$; Fig. 2).

One-way ANOVA and the Tukey-Kramer Honestly Significant Difference (HSD) tests were applied to compare mean standard lengths of prey among seven time periods for both *Pleuragramma antarcticum* and *Psychroteuthis glacialis* ($P = 0.05$). The Tukey-Kramer (HSD) test was applied to reduce potential errors in significance (Sall et al. 2001).

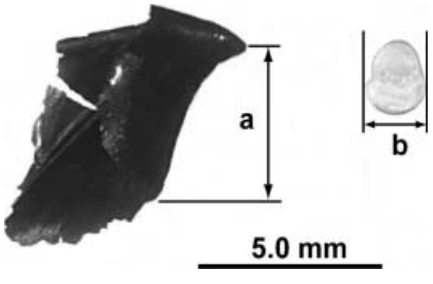


**Fig. 2.** Measurements of lower rostral length (LRL, *a*) on a beak of *Psychroteuthis glacialis*, and otolith width (OW, *b*) on *Pleuragramma antarcticum*

## Results

Among the five study sites, seven occupation periods are represented, including a modern period of less than 400 years (Emslie and McDaniel 2002). These dates indicate that Adélie penguins first occupied Lagoon Island at approximately 6000 BP following a deglaciation event (Emslie 2001). Occupation and abandonment thereafter is correlated with glacial retreats and advancements, and Lagoon Island was permanently abandoned by 895–650 BP. Ginger Island was first occupied by Adélie penguins as early as 2275 BP; however, the island was probably abandoned from 1900 to 720 BP. Reoccupation of Ginger Island occurred from 720 to 405 BP and appears to have been continuous from that time (Emslie and McDaniel 2002).

Dietary remains were quantified per time period based on the occupation history. Eight families and 32 taxa of fish are represented in the sites, with *Pleuragramma antarcticum* as the most represented and abundant prey species identified. Two taxa of squid, *Psychroteuthis glacialis* and *Brachioteuthis* sp., are well represented in the younger deposits while mostly unidentifiable fragments are found in the older time periods (Emslie and McDaniel 2002).

Mean SL for *Pleuragramma antarcticum* varied from a low of $95.0 \pm 22.56$ at 720–405 BP to a high of $110.32 \pm 26.89$ at 1490–1220 BP (Fig. 3A); the mean SL for all time periods was $108.19 \pm 25.53$ mm (range 15.82–187.4 mm). Mean SL in the modern time period was significantly different from all time periods except 2750–1715 BP and 3975–3265 BP (ANOVA, $df = 6$, $P = 0.002$; Fig. 3A). The 720–405 BP and 895–650 BP time periods were significantly different ($P = 0.0020$) from all other time periods, but not from each other. No significant differences were found between mean SLs of the remaining time periods.

*Psychroteuthis glacialis* beaks (Fig. 3B) from the modern and 720–405 BP time periods were the only measurable specimens, since the older deposits contained only beak fragments. Estimated mean ML from the modern time period ($101.54 \pm 33.94$ mm) was significantly shorter than that of the 720–405 BP period ($116.92 \pm 28.79$ mm; ANOVA, $df = 1$, $P = 0.0035$; Fig. 3B). The total estimated mean ML for both time periods was $110.72 \pm 31.77$ mm (range 28.79–197.04 mm).

## Discussion

Although krill (*Euphausia superba*) is the primary component of Adélie penguin diet (Williams 1995), fish and squid also can be important depending on seasonal availability. For example, Puddicombe and Johnstone

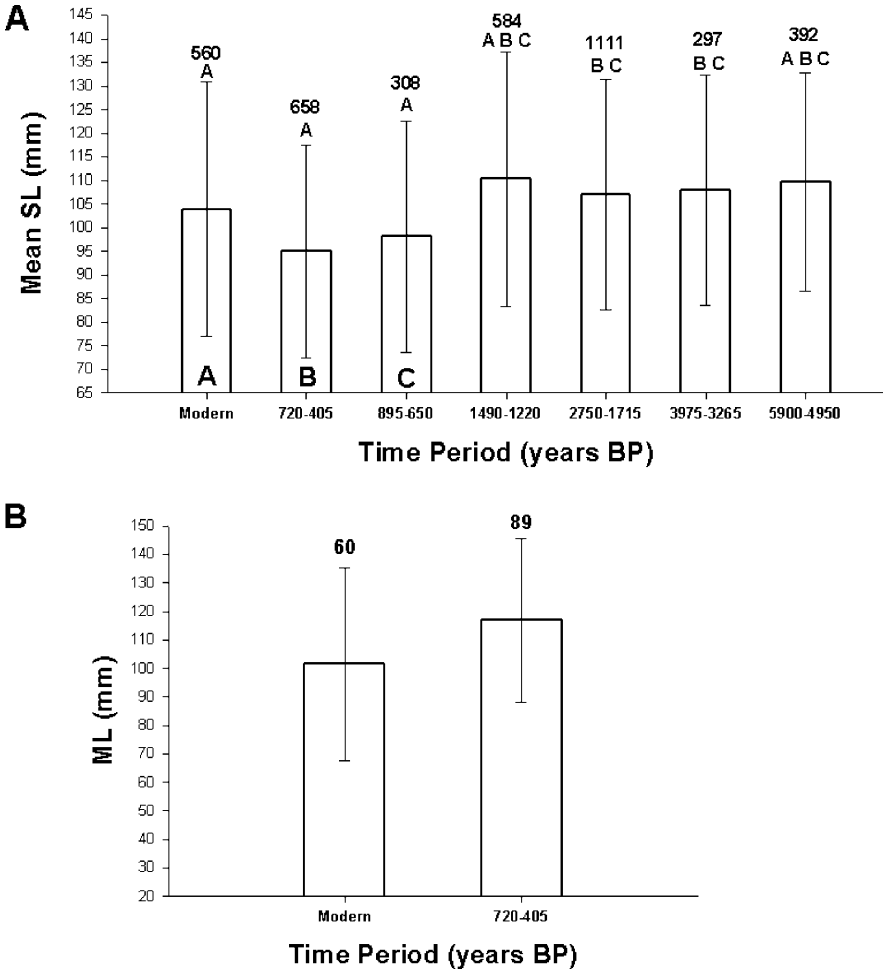


**Fig. 3.** **A** Mean standard lengths ($SL$) ± standard deviations of *Pleuragramma antarcticum* based on otolith measurements from ornithogenic sediments dating to each of seven time periods in northern Marguerite Bay. *Numbers* above *bars* are sample sizes. Bars for the modern, 720–405 BP, and 895–650 BP time periods are labeled *A*, *B*, and *C*, respectively. Shared *letters* above other bars indicate a significant difference ($P = 0.002$) between those three labeled bars. **B** Mean mantle lengths ($ML$) ± standard deviations of *Psychroteuthis glacialis* based on beak measurements from ornithogenic sediments dating to the modern and 720–405 BP time periods. These means are significantly different ($P = 0.0035$). *Numbers* above *bars* are sample sizes

(1988) found a noticeable shift in Adélie penguin diet to Antarctic silverfish (*Pleuragramma antarcticum*) later in the season at the Vestfold Hills during one breeding season. Little is known on the importance of cephalopods in the diet of Adélie penguins (Clarke 1986), but the Antarctic squid (*Psychroteuthis glacialis*) has been recorded in diet samples at Adélie Land (Offredo et al. 1985). In addition, a variety of squid taxa, but especially *Psychroteuthis glacialis*, regularly occur in ornithogenic sediments at abandoned and active penguin colonies in the Antarctic Peninsula, suggesting that cephalopods compose a significant portion of penguin diet, at least during part of the breeding season (Emslie et al. 1998; Emslie and McDaniel 2002).

In northern Marguerite Bay, Antarctic silverfish was the most abundant species represented in all time periods (Emslie and McDaniel 2002). This fish is a key component of the Antarctic marine ecosystem and its role in the food web is similar to krill. Antarctic silverfish are the most abundant nekton in the Weddell Sea and constitute 90% of the midwater fish biomass in the Ross Sea (Guglielmo et al. 1998).

The range of prey-size estimates for *Pleuragramma antarcticum* demonstrates that mostly juvenile silverfish are represented in the Rothera sediments (Fig. 3A). Juvenile silverfish with SL = 33–110 mm are found primarily at depths of 50–400 m (Hubold 1984; Wöhrmann et al. 1997) and feed in krill swarms distributed in the upper 100 m of the water column (Rembiszewski et al. 1978; Nast et al. 1987; Watkins and Murray 1998). Adélie penguins forage at depths between 3 and 98 m (Chappell et al. 1993), though they are known to reach depths of 170 m (Williams 1995 citing Wilson et al. 1989); therefore, juvenile silverfish are an accessible and valuable food source for penguins. It is possible that penguins are incidentally catching silverfish while feeding on krill, thereby explaining the abundance of *Pleuragramma antarcticum* otoliths in the ornithogenic sediments. Another explanation for high silverfish abundance is that Adélie penguins compensate for low krill years by targeting different prey species, such as *Pleuragramma antarcticum* and/or *Psychroteuthis glacialis*, as suggested by Ainley et al. (1998) and Emslie et al. (1998).

Temporal variations within the juvenile silverfish size range do not reflect a predictable cycle in concert with climate change. For instance, warming events, such as the glacial retreat from 6000 to 5000 BP and the "penguin optimum" (4000–3000 BP; see Emslie and McDaniel 2002), are characterized by relatively large silverfish (Fig. 3A). However, the mean SL of silverfish

was also high during the cooling episode that occurred at 2750–1220 BP. Glacial oscillations at 895–405 BP lack the resolution of the earlier climate record; however, silverfish consumed during these periods were significantly smaller in size in comparison to all other time periods (Fig. 3A).

Despite the lower nutritional value of squid compared to krill and fish (Croxall and Prince 1982a, b), modern dietary studies have shown that penguins do prey upon them (Offredo et al. 1985; Puddicombe and Johnstone 1988; Ridoux and Offredo 1989; Ainley et al. 1992). As with the silverfish, Adélie penguins may be taking squid only while feeding in krill swarms where squid also prefer to prey on krill (Offredo et al. 1985). The most common species of squid represented in the sediments, *Psychroteuthis glacialis*, is mesopelagic and found at depths ranging from 200 to 700 m (Sweeney et al. 1992); however, larval forms (4–18 mm) have been found at shallow depths (exact depth not specified; Lu and Williams 1994). This squid lives approximately 1 year from hatching (July to September) to spawning, and is depredated by both emperor and Adélie penguins. During the spring (October/November), *Psychroteuthis glacialis* is eaten by adult emperor penguins. However, Adélie penguins may not begin feeding on squid until February (see Offredo et al. 1985).

The majority of the *Psychroteuthis glacialis* specimens recovered here were fragmented. However, specimens from the modern and 720–405 BP time periods indicate a smaller relative prey size in the former period. This change is difficult to interpret without additional periods for comparison. The mean MLs are comparable in size to the mean SLs of Antarctic silverfish, indicating that Adélie penguins primarily select non-krill prey within a mean size range of 95–117 mm, though sample ranges are much broader and extend up to 187.4 and 197 mm for silverfish SL and squid ML, respectively. Comparative data of non-krill prey from abandoned colonies in other areas are needed to determine which factors control temporal variation of prey size in Adélie penguins.

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