

Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference?

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ABSTRACT: Macaroni *Eudyptes chrysolophus* and gentoo *Pygoscelis papua* penguins occur sympatrically at Bird Island (54° 00' S, 38° 02' W), South Georgia, and have a similar diet. Macaroni penguins forage at shallower depths and further from the island than gentoo penguins. We tested the hypothesis that differences in the optimal foraging behaviour at the level of individual dives help to explain this ecological foraging segregation. Using a rate maximising diving model, we predicted that macaroni penguins would obtain more energy per dive cycle than gentoo penguins only when they used patches shallower than 30 to 40 m. This prediction was supported by observations of actual dive depths. We conclude that different foraging efficiencies at different depths results in each species being differentially sensitive to the vertical distribution of prey in the water column. We suggest that differing capacities to exploit natural heterogeneity in the distribution of prey has an important role in maintaining these 2 species as sympatric predators of a common resource.

KEY WORDS: Optimal foraging · Segregation of foraging area · Macaroni penguins · Gentoo penguins

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INTRODUCTION

Gause's theory of competition predicts that, when species depend upon a common food resource, they either evolve to exploit different parts of the resource or one species excludes the other from the resource. Although some species are excluded by interspecific competition from locations in which they could exist in the absence of competition, competing species also often appear to coexist by spatio-temporal segregation, even though they exploit the same freely mixing prey population (Townsend et al. 2000). In these circumstances, it appears that competition must still exist but that trade-offs in physiological, morphological, and/or behavioural traits maintain an equilibrium between species, permitting coexistence despite interspecific competition (Tilman 1987). Several studies have recently investigated the role of differences in foraging

behaviour among competing species, and have found that differences in foraging behaviour and efficiency are important for coexistence in communities of seabirds (e.g. Ballance et al. 1997), fishes (e.g. Nakano et al. 1999, Persson & Bronmark 2002) and small terrestrial mammals (e.g. Brown 1989, Jones et al. 2001).

If the behaviour of predators tends to converge towards an optimal solution for a particular environment, the optimum for different species will differ according to species-specific physiological and morphological constraints. This may be 1 reason for the development of a guild of predators that is largely dependent upon krill *Euphausia superba* in the Southern Ocean (Laws 1977). Both whales and seals are represented amongst this guild, with a body size range spanning almost 5 orders of magnitude and including raptorial and filter methods of feeding. It has also been suggested that seabirds feeding on krill in the South-

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ern Ocean are ecologically segregated because of differences in morphological, physiological and/or behavioural adaptations (Croxall & Prince 1980, Laws 1985). In the present paper we tested the hypothesis that differences in the foraging behaviour of 2 species help to explain this ecological segregation. By studying different species, we aimed to examine extremes of behaviour in a range of phenotypes that are driven by selection at the level of individuals, but which may also apply to different phenotypes within species.

We focused on 2 penguin species, macaroni penguins *Eudyptes chrysolophus* and gentoo penguins *Pygoscelis papua*. If interspecific differences in physiological and environmental constraints exist, then in order to forage optimally, diving animals should have segregated foraging depths (Mori 1998, 2002). Therefore, we predicted that these sympatric penguins would differ in their preferences for certain foraging depths even after allowing for differences in prey abundance at these depths.

Our study area was Bird Island, South Georgia, where gentoo penguins feed mainly on krill (70% by weight) and some fishes, and macaroni penguins feed almost exclusively on krill (97% by weight) in most years (Croxall et al. 1997). There is no significant difference in the length of krill caught by these penguins (Reid et al. 1996, Croxall et al. 1997). However, macaroni penguins forage further from the island (5 to 80 km) and at shallower depths (around 30 m) than gentoo penguins (<30 km and 50 to 80 m) (Croxall & Prince 1980, Williams 1991, Hunt et al. 1992, Williams et al. 1992a,b, Croxall et al. 1993, 1997, Barlow et al. 2002). This indicates that there may be spatial segregation between foraging macaroni and gentoo penguins even when foraging on a common resource.

MATERIALS AND METHODS

Data collection and processing. Dive data were collected from breeding macaroni and gentoo penguins during the austral summer of 1992/93 at Bird Island (54° 00' S, 38° 02' W), South Georgia (see Davis et al. (1989) for detailed ecological information on these penguins in the study area). Dive data were recorded by electronic time-depth recorders (TDR, Mk 5, Wildlife Computers). The recorders were attached to the birds' feathers on the rump with waterproof tape and epoxy glue. This allowed the device to be removed after deployment with minimum disturbance to the birds. In the case of gentoo penguins, the TDR was attached to 1 member of a brooding pair immediately after the end of its incubation shift and before it returned to sea. The TDR was recovered when the bird returned to take up its next incubation shift. In the case

of macaroni penguins, TDRs were placed on females during their brooding foraging trips (Davis et al. 1989). We collected dive data from 7 macaroni penguins and 5 gentoo penguins that foraged for 2 to 5 d. In all cases the TDRs measured depth (± 0.5 m) at intervals of 5 s when penguins were in the water.

The time series of diving behaviour was reconstructed using purpose-built software. A depth of 2 m was set as the threshold below which penguins were assumed to have dived. Dive time, maximum depth, bottom time and surface time following the dive were calculated. We defined bottom time as the difference between the time when the descent ended and ascent began. Our definition of 'bottom time' does not necessarily mean time spent at a constant depth or during the flat part of a U-shaped dive. The bottom time was considered to be related to feeding (e.g. Charrassin et al. 2001). Travel time was defined as descent time plus ascent time. The termination of the descent was defined as the point at which the rate of descent decreased to less than the mean rate of descent, measured between the point at which the maximum depth was reached during the dive and the surface at the start of the dive. (We assumed that the rate of descent would be rapid from the water surface to a foraging patch, but would slow down when the birds found a prey patch and began to forage.) The commencement of ascent was defined as the point at which the rate of ascent first exceeded the mean rate of ascent.

We split sequential dives into dive bouts according to the criterion of sequential differences analysis (Mori et al. 2001): if the difference in the preceding surface time between a dive and a previous dive was larger than the criterion, then the 2 dives were separated into different dive bouts. The criteria from the sequential differences analysis were 78.3 and 148.8 s for macaroni and gentoo penguins, respectively.

Dive bouts were assumed to indicate foraging activity within a prey patch. When a dive bout consisted of 1 dive we refer to this as a 'single dive', and when a dive bout consisted of multiple dives we refer to the dive bouts and the dives within the bout as 'foraging bouts' and 'bout dives', respectively. In total, we split 5089 and 1770 dives of 7 and 5 individuals into 652 and 93 dive bouts for macaroni and gentoo penguins, respectively. Foraging bouts and single dives accounted for 318 bouts and 334 dives for macaroni penguins, and 52 bouts and 41 dives for gentoo penguins. Single dives were excluded from further analysis because these dives were considered to be searching or unsuccessful foraging dives.

Optimal time allocation during a dive cycle. Here we describe a model, based on that of Mori et al. (2002), which concerns optimal time allocation during a dive cycle for penguins foraging in a patch for which patch depth and quality are known.

A dive cycle consists of dive time, u , and surface time, s . Since the penguins need to surface to replenish their oxygen reserves during diving, the surface time is a function of the dive time: $s = y(u)$. This function describes a physiological constraint that limits the time budgets of the diving birds, and is assumed to be an accelerative increasing function. The dive time consists of 2 variables: time spent in a prey patch, f , and the travelling time from the surface to the prey patch and back, t . In general, travelling time corresponds to dive depth. Thus, it follows that

$$u + s = f + t + y(u) \quad (1)$$

where $y'(u) > 0$ and $y''(u) > 0$.

The amount of energy taken during a dive cycle, g , is a function of time spent in a foraging patch, f . We assumed that this function is a power function of time spent in a foraging patch, or

$$g = a \cdot f^x \quad (2)$$

where parameter a represents a coefficient of conversion of time into actual energy intake. Although we do not know the exact relationship between the amount of energy intake and time spent in a foraging patch, it seems reasonable to assume that the rate of energy intake declines through a dive because of factors such as depletion of the prey patch by the predator and escape responses by the prey. The power function covers all options of increasing (decelerating, constant and accelerating) by setting exponent $x < 1$, $= 1$, or > 1 . Since exponent x affects the amount of energy intake per unit time, this exponent can represent the quality of a patch used by the diving predator. We call this exponent the 'index of patch quality' (IPQ). Since $f = u - t$, the amount of energy intake during a dive cycle, G , is

$$G = g/(u + s) = a \cdot (u - t)^x / [u + y(u)] \quad (3)$$

We assumed that the penguins attempt to maximise energy intake during a dive cycle, G , and that the penguins would therefore choose an optimal dive time, u^* , for a given travelling time, t , and patch quality, x , at the depth corresponding to the travelling time. The parameter a made no contribution to the choice of optimal dive time or to the effects of any other variable when maximising Eq. (3) in the calculation. To investigate the relative difference in energy intake between macaroni and gentoo penguins, we set a at 1, because although this parameter may depend upon the feeding methods of the predator or the energetic value of a prey item, there seemed to be little difference in these aspects between macaroni and gentoo penguins. We assumed that prey swimming speed was not a significant factor affecting the foraging tactics of the penguins. In some circumstances, the swimming speed of prey can affect opti-

mal time allocation during dive cycles (Wilson et al. 2002). In our study area, both penguins feed on the same type of prey, so we assume that swimming speed associated with prey capture has little effect on the interspecific comparison. In addition, krill are not fast swimmers relative to the diving speed of these predators, so any effect of swimming speed is likely to be small.

By comparing the energy intake during a dive cycle for various depths and by adjusting the travelling time and patch quality between the 2 penguin species, we investigated which species was most successful in competing for the same prey resource as a function of foraging depth and patch quality.

Estimation of vertical distribution of patch quality.

In order to examine the relative profitability of foraging by each penguin species in different parts of the water column, it was necessary to obtain an estimate of the vertical distribution of prey. There were no synoptic data for this distribution from hydroacoustic surveys that coincided with this study; therefore we used the vertical profile of the estimated IPQ of Antarctic fur seals *Actocephalus gazella* that were foraging in the same region and at the same time as our study birds, to represent the vertical distribution of prey. The IPQ measured for fur seals has previously been shown to be closely related to the abundance of krill measured by ship-based hydroacoustic surveys (Mori & Boyd 2004).

Antarctic fur seals at Bird Island also eat krill and forage sympatrically with both macaroni and gentoo penguins (Barlow et al. 2002, Boyd et al. 2002). Their diving capacity is similar to that of these penguins: the maximum dive time of Antarctic fur seals is 180 to 240 s (Boyd & Croxall 1992), while that of the macaroni and gentoo penguins in the present study was 150 to 286 and 158 to 280 s, respectively. Antarctic fur seals also forage in the area covering the range of macaroni penguins (Barlow et al. 2002), which forage further than gentoo penguins (Croxall et al. 1993). The size distribution of krill caught by fur seals and by fishing nets is broadly similar (Reid & Arnould 1996, Reid et al. 1996), suggesting fur seals are effective and unbiased samplers of the krill population or that they are biased in the same ways as fishing nets. Therefore, the vertical distribution of the IPQ experienced by fur seals can be taken to be the same as that experienced by macaroni and gentoo penguins (see also 'Discussion'). Estimating prey patch quality from diving behaviour has also been discussed by Mori et al. (2002).

The principal of measuring the IPQ is that, in diving animals, variation in bottom time for a given travelling time or dive depth should reflect variation in the quality of the exploited prey patch (Mori et al. 2002). We estimated the IPQ as follows: We assumed that fur seals adjusted their dive time to maximise their energy

intake during a dive cycle, G , for a given travelling time, t , and the IPQ, x . From the regression equation for dive time and the shortest succeeding surface time required, we estimated the relationship between dive time and surface time, $y(s)$, for fur seals as $s = -33.3 \ln(1 - 0.0044u)$. This function was substituted into Eq. (3). Since dive time, u , and travelling time, t , were obtained by observation, and we assumed that fur seals maximised their energy intake (Eq. 3), we could determine the IPQ to which fur seals adjusted their dive time for a given travelling time by seeking the exponent x which maximised Eq. (3). Dive data from fur seals were obtained from 18 individuals during the austral summer in 1992/93. Capture methods followed those of Gentry & Holt (1982), and the devices were attached by the method of Boyd & Croxall (1992). We used the same devices to record the diving behaviour of fur seals as those used for penguins, and data processing followed the same procedure as that for penguins. In total, we recorded 3684 foraging bouts for foraging Antarctic fur seals. We assumed that each dive bout corresponds to a single prey patch (Boyd 1996, Hooker et al. 2002). Therefore, we regarded each foraging bout as an independent prey patch in the analysis. These foraging bouts were used for estimate of vertical distribution of the IPQ.

We calculated the IPQs for all dives and obtained the mean IPQ from dive bouts made by fur seals. This mean IPQ during a dive bout was assumed to be the IPQ of the krill patch. We also calculated the mean dive depth during a dive bout, which we considered to represent patch depth. We could then obtain the vertical distribution of the IPQ of krill patches used by fur seals at Bird Island, and regarded this as representing the vertical distribution of the IPQ of krill patches in the areas in which macaroni and gentoo penguins foraged.

RESULTS

Time budgets and physiological constraints

For diving bouts with the same mean dive times but with different mean surface times, we used the bout duration associated with the shortest mean surface time to determine the relationship between dive and surface duration. The mean surface time within a diving bout was positively correlated with the mean dive time within a bout for both species (Fig. 1, Student's t -test; $t = 16.6$, $df = 120$, $p < 0.0001$; and $t = 2.2$, $df = 42$, $p = 0.03$, for macaroni and gentoo penguins, respectively). When expressed as the mean for each bout, surface time was shorter for macaroni penguins than for gentoo penguins when dive time was short (<80 s).

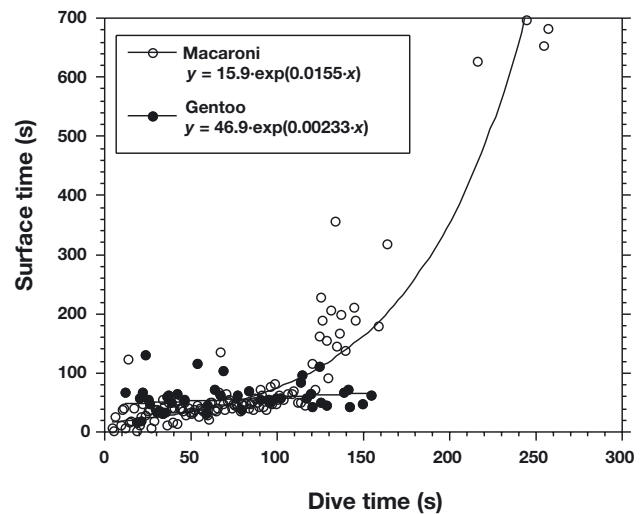


Fig. 1. *Eudyptes chrysolophus* and *Pygoscelis papua*. Mean dive time and surface time within a foraging bout. Pooled data from different individuals. Regression curves and equations are shown

However, surface times associated with long dive times were much longer for macaroni penguins than for gentoo penguins (Fig. 1). Maximum dive depth and travel time during dives were correlated positively in all individuals of both species. The regression coefficient a in the equation travel time = $a \times$ depth was 0.83 to 1.59 ($n = 9$ to 111, $R^2 = 0.57$ to 0.96) and 0.89 to 1.21 ($n = 8$ to 18, $R^2 = 0.94$ to 0.99) for macaroni and gentoo penguins, respectively. There was no significant difference in these coefficients between species (t -test; $t = 1.7$, $df = 10$, $p = 0.12$), and the mean coefficient was 1.09. This shows that travel time varied in direct proportion to depth.

The regressions of surface time with dive time reflected the physiological constraints associated with diving in the 2 penguin species; this corresponds to $y(u)$ in Eq. (3). We used this to calculate the expected maximum energy intake per dive cycle given by the optimal allocation of time during the dive cycle. This calculation was repeated for various dive depths (1 to 80 m) and IPQs (0.1 to 1.0) for each species, using the equation travel time = $1.09 \times$ depth for conversion of dive depth to travel time. This revealed that macaroni penguins are likely to achieve a greater energy intake rate per dive cycle than gentoo penguins when the prey patch is shallow and the IPQ is low (Fig. 2). This suggests that physiological constraints on the 2 species differ and that macaroni penguins are able to forage more profitably on shallow prey than gentoo penguins. The depth threshold at which there was a switch in foraging profitability between the 2 penguins declined as dive depth increased (Fig. 2).

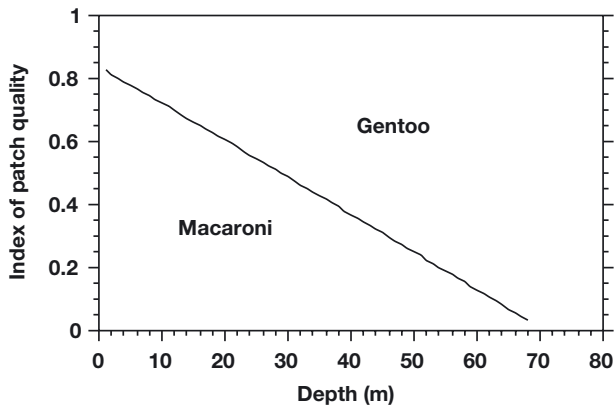


Fig. 2. *Eudyptes chrysolophus* and *Pygoscelis papua*. Effects of foraging depth and patch quality on the species which achieves a larger energy intake during an optimal dive cycle. Macaroni penguins theoretically achieve a larger energy intake during an optimal dive cycle than gentoo penguins in patches characterised by the region below the line

Vertical distribution of the IPQ

The vertical distribution of the IPQ estimated in the study area using data for Antarctic fur seals revealed that the IPQ increased from 0 to 0.5 as depth increased down to 25 m, and remained relatively stable thereafter until 70 m, whereafter it appeared to decline slowly with increasing depth (Fig. 3). The IPQ threshold at which a switch in foraging profitability between macaroni and gentoo penguins occurred was around a depth of 30 to 35 m (Fig. 3), suggesting that in the study area macaroni penguins can forage more profitably than gentoo penguins when patches are shallower than 30 to 35 m, while gentoo penguins would have an advantage when prey patches are deeper than 30 to 35 m.

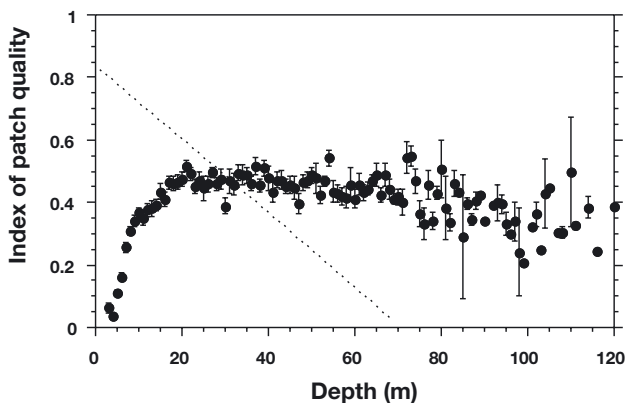


Fig. 3. Vertical distribution of index of krill patch quality estimated from diving behaviour of Antarctic fur seals *Actocephalus gazella*. Dotted line: threshold at which a switch in foraging profitability of species in interspecific competition was predicted to occur (see Fig. 2)

Diving performance

The frequency distribution of the depth of foraging bouts (Fig. 4) showed an overall significant difference in the depth of patches used for foraging between the 2 penguin species (χ^2 -test for pooled data, $\chi^2 = 61.7$, $df = 9$, $p < 0.0001$). More than 90% of the prey patches used by macaroni penguins were shallower than 40 m, while nearly half (46.1%) of the prey patches used by gentoo penguins were between 40 and 90 m; however, 35% of patches used by gentoo penguins were relatively shallow (0 to 10 m). This pattern of bout-depth distribution was observed for each individual. The percentage of prey patches deeper than 40 m relative to all prey patches used by each bird was 0 to 25% (mean \pm SE: 8.8 ± 4.2 , $n = 7$, median = 5.6) and 28 to 62% (49.0 ± 5.7 , $n = 5$, median = 50.0) for macaroni and gentoo penguins, respectively, and the difference was significant (Mann-Whitney U -test; $U = 35$, $z = 2.87$, $p < 0.01$). This suggests segregation in foraging depth between the 2 penguin species at Bird Island.

Estimates of energy intake per dive cycle calculated from observed bottom time, dive time and vertical distribution of the IPQ showed that macaroni penguins achieved a higher estimated energy intake per dive cycle when dive depth was between 30 and 40 m, while the estimated energy intake of gentoo penguins

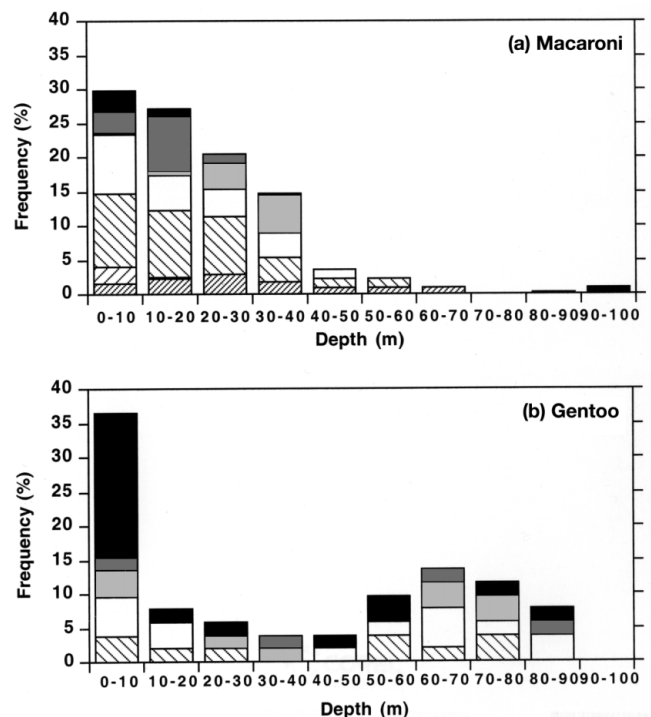


Fig. 4. (a) *Eudyptes chrysolophus*; (b) *Pygoscelis papua*. Frequency distribution of mean depth of foraging bouts. Different patterns represent different individuals. In total, $n = 318$ and 52 for macaroni and gentoo penguins, respectively

exceeded that of macaroni penguins when prey patches were deeper than 40 m (Fig. 5a). Grouping the foraging bouts into shallow (<40 m) and deep (\geq 40 m) bouts revealed that, although there was no significant overall effect of species and bout depth on the estimates of energy intake rate during a foraging bout, there was a significant interaction between species and bout depth (2-factor ANOVA for pooled data; effect of depth: $df = 1,366$, $F = 0.65$, $p = 0.42$, effect of species: $df = 1,366$, $F = 1.32$, $p = 0.25$, interaction: $df = 1,366$, $F = 26.14$, $p < 0.0001$) (Fig. 5b).

DISCUSSION

Assumptions used in model

When developing the model, we made some assumptions about optimal diving behaviour. Firstly, we assumed that energy intake was a power function of bottom time. Some studies have shown that undulations during the bottom phase of the dive indicate

feeding by penguins (Kirkwood & Robertson 1997, Ropert-Coudert et al. 2000, Simeone & Wilson 2003). In the present study, it was not possible to record the exact number of undulations because of the relatively long sampling interval (5 s), so we assumed that the duration of bottom time was associated with the amount of energy intake. Mori et al. (2002) showed that developing a similar foraging model using a power function provided a satisfactory explanation of diving behaviour in Brünnich's guillemots *Uria lomvia*. Even in circumstances in which this assumption about the functional form may not be upheld, such a power function will approximate the asymptotic and decelerating nature of energy intake with time spent in a foraging patch by a predator. Therefore, we would not expect the results to be highly sensitive to the functional form, as long as the rate of energy intake is an asymptotic and decelerating function. However, we have assumed that the functional form was similar in the 2 species of penguins.

Secondly, we estimated the vertical distribution of patch quality from the diving behaviour of Antarctic fur seals whose foraging range and diving capability overlapped with those of both species of penguins. This also assumed that fur seals adjusted their dive cycle optimally as rate-maximisers, probably at the scale of the dive cycle (see Boyd et al. 1995). In addition, inter-annual variation in estimates of patch quality based on the diving behaviour of Antarctic fur seals at Bird Island was positively correlated with that of krill density measured in ship-based hydroacoustic surveys around Bird Island (Mori & Boyd 2004). Also, the effect of krill density on reproductive success was similar between Antarctic fur seals and the 2 penguin species at Bird Island (Boyd & Murray 2001). This indicates that the krill distribution experienced by fur seals could be the same as that experienced by the macaroni and gentoo penguins. Therefore, the estimates of the vertical distribution of the IPQ in the study area using the diving behaviour of fur seals are likely to provide a guide to the vertical distribution of krill in the water column (see also below). Antarctic fur seals foraged mainly at night, when krill are at relatively shallower depth, while the penguins foraged during the day, when krill are deeper in the water column. However, the vertical distribution of krill density (which can be represented by the IPQ) seemed rather constant between 20 and 70 m (Fig. 3). Therefore, even if night-time krill patches move to a deeper layer in the water column in the daytime, the depth threshold at which there is a switch in the relative foraging profitability of the 2 species remains around 30 to 40 m.

Thirdly, we assumed that penguins adjusted their dive cycle optimally for given depths and patch qualities. Using the estimated vertical distribution of the

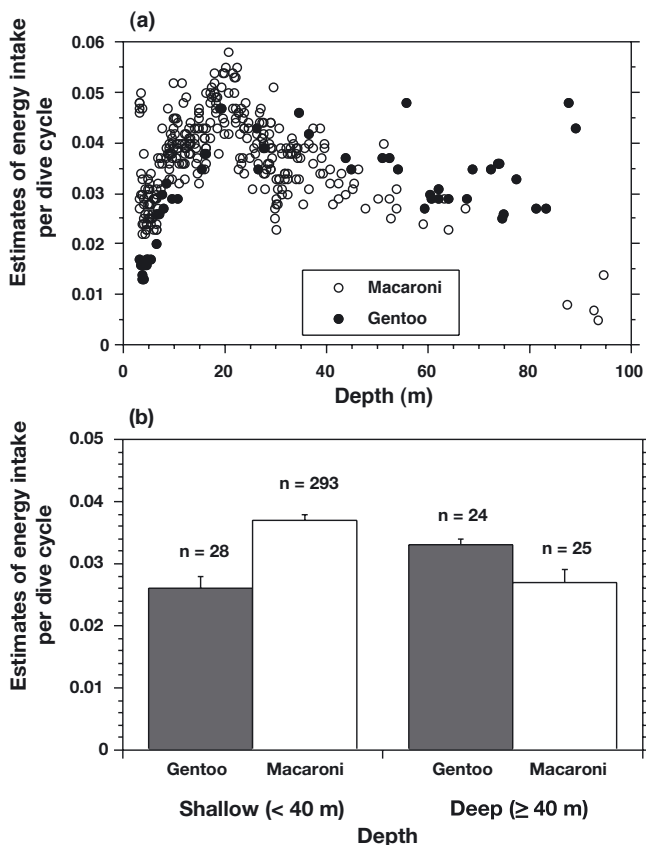


Fig. 5. *Eudyptes chrysolophus* and *Pygoscelis papua*. (a) Estimates of energy intake per dive cycle in relation to foraging depth; (b) mean (+SE) estimated energy intake rates during diving bout as a function of foraging-depth intervals. Pooled data from various individuals

IPQ, we calculated the optimal dive time for each depth for each species, and compared these with the observed distribution of dive times. Although the observed dive time was slightly longer and shorter than the calculated optimal dive times for macaroni and gentoo penguins, respectively, the overall tendency showed that the observed dive time was positively correlated with the optimal dive time ($n = 18$, $F = 82.3$, $df = 1, 17$, $p < 0.0001$, $R^2 = 0.827$), and the slope of the regression line was 1.009 (Fig. 6). This indicates that, overall, the observed dive time was similar to the optimal dive time estimated from the vertical distribution of the IPQ (as determined from the behaviour of fur seals), supporting the assumption that the penguins adjusted their dive cycle optimally as rate-maximisers. This also indicates that the vertical distribution of IPQ estimated from the behaviour of fur seals was similar to that experienced by penguins in the present study. Therefore, the assumptions used in the model appeared to be reasonable and appropriate for investigating the diving behaviour of penguins.

Segregation of depth use and optimal diving behaviour

We found that macaroni penguins mainly used patches shallower than 40 m while gentoo penguins used deeper patches (Fig. 4). Gentoo penguins also displayed many shallow bouts of diving (0 to 10 m). These bouts may not have been actual foraging bouts, but searching or travelling dive bouts, because (1) the median number of dives per bout for these bouts (7.0) was smaller than that for deeper bouts (28.0, Mann-Whitney U -test: $U = 119.5$, $p < 0.001$); (2) 63% of single dives, which we assumed to be searching, travel-

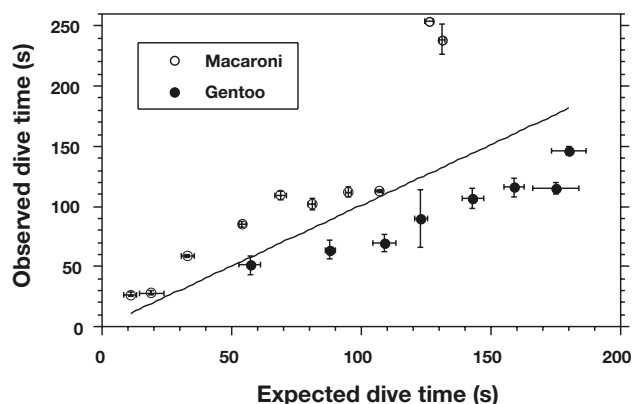


Fig. 6. *Eudyptes chrysolophus* and *Pygoscelis papua*. Expected dive time predicted by optimal foraging theory and observed dive time as a function of depth (10 m depth intervals). Means \pm SE. Regression line for pooled data is shown

ling or unsuccessful dives, were shallower than 10 m ($n = 41$, median = 4.0 m); (3) the IPQs of 0 to 10 m were very low (Fig. 3). Williams et al. (1992a) also suggested that most shallow dives are searching/exploratory dives in gentoo penguins in South Georgia. Thus, we conclude that there is segregation by depth of foraging (and exploitation related with foraging) between macaroni and gentoo penguins at Bird Island, with macaroni penguins using shallower patches and gentoo penguins deeper patches. This is consistent with previous studies that examined differences between these species at the level of dives rather than bouts (Croxall et al. 1993).

The surface time for dives longer than 120 s increased rapidly in macaroni penguins, suggesting that in the present study the aerobic dive limit (ADL, Kooyman 1989) of macaroni penguins was around 120 s. In contrast, gentoo penguins seemed to be able to dive aerobically for at least 150 s (Fig. 1). Macaroni penguins, however, are capable of diving to at least 100 m (this study and Croxall et al. 1993) and appear to move through geographical regions in which the gentoo penguins forage (Croxall et al. 1993, Barlow et al. 2002). These 2 penguin species have similar diets, and consume similar-sized krill (Reid et al. 1996, Croxall et al. 1997). Thus, macaroni penguins appear to have the opportunity and physiological capability of foraging in the same locations as gentoo penguins, but probably cannot do so at the same level of profitability. Foraging segregation in the 2 species may represent different solutions to a trade-off between distance of prey from the nest and depth of prey. Based on the physiological constraints of the 2 species and the distribution of prey in the water column, we predicted that macaroni penguins could obtain more energy intake per dive cycle than gentoo penguins only when they used patches shallower than 30 to 40 m (Figs. 3 & 5). This prediction was consistent with our observation that foraging depth segregation occurred at around 40 m (Fig. 4). Our findings suggest that gentoo penguins are able to profitably exploit a relatively large proportion of the water column and will therefore have a comparatively large choice of prey patches close to the colony. In contrast, macaroni penguins appear to have to travel further to find prey, because they exploit a relatively small proportion of the water column. At Bird Island, the foraging area of flying birds such as albatrosses (*Diomedea* spp.), which can only forage on the surface, is also much greater than that of macaroni penguins (Croxall & Prince 1980, Croxall et al. 1997). This observation is consistent with the prediction that the foraging area will be greater for birds foraging at shallower depths. Therefore, we conclude that the segregation by foraging depth and area found for these 2 penguin species at Bird Island probably arises from differences

in their optimal foraging depth in relation to the vertical distribution of prey patches. This factor is likely to facilitate the stable coexistence of these 2 species in the same region; however, such coexistence is likely also to rely upon the retention of relatively high densities of krill above and below the depth threshold at which there is a switch in the relative foraging profitability for the 2 species.

Therefore, we predict that the relative success of gentoo and macaroni penguins during the breeding season may depend not only upon the absolute level of prey available but also upon its vertical distribution. Prey at greater depths will benefit gentoo penguins more than macaroni penguins, but only when relatively close to the colony; macaroni penguins will be at an advantage when prey are concentrated closer to the surface.

Adélie *Pygoscelis adeliae* and chinstrap *P. antarctica* penguins breeding in Signy Island showed niche differentiation in foraging behaviour; Adélie penguins ate smaller krill (Lishman 1985) at a greater range from the colony than chinstrap penguins (Lishman 1985, Lynnes et al. 2002). These studies did not provide data on dive-depth segregation, but Lynnes et al. (2002) suggested that the occurrence of segregation in a foraging area depended upon prey availability and differential abilities of the penguins to cope with changing ice conditions. Royal penguins *Eudyptes schlegeli* and rockhopper penguins *E. chrysocome* breeding on Macquarie Island have different diets as well as different foraging areas (Hull 2000). There is a slight difference in their use of the water column, but segregation in this respect is far from complete (Hull 2000). It is possible that, unlike macaroni and gentoo penguins at Bird Island, the only means of coexistence at Macquarie Island is for the species to capture different prey.

In conclusion, macaroni penguins and gentoo penguins breeding at Bird Island forage under different physiological constraints, resulting in different foraging efficiencies which make each species differentially sensitive to the vertical distribution of prey in the water column. This results in foraging depth segregation, and thus presumably foraging area segregation of the 2 penguin species. It seems likely that this difference plays an important role in maintaining these 2 species as sympatric predators of a common resource. The coexistence of these species may be maintained by their different capabilities for exploiting the natural heterogeneity in the distribution of prey. Although the present study examined the effects of differences in optimal foraging behaviour on ecological segregation at the interspecific level, we expect that the same pattern will exist for different phenotypes within species and that intra-specific competition will also be influenced by the same process.

Acknowledgements. This work was partly funded under grant GR0003 of the NERC Antarctic Funding Initiative. A. Takahashi, Y. Watanuki and anonymous reviewers provided valuable comments on the manuscript.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

*Submitted: October 6, 2003; Accepted: March 18, 2004
Proofs received from author(s): June 23, 2004*