ARE THERE STRUCTURAL DIFFERENCES IN THE FLIGHT FEATHERS AMONG PROCELLARIIFORMES RELATED TO THE USE OF WINGS FOR UNDERWATER PROPULSION?

by

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Table of Contents

PLAGARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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My family and friends for their consistent love and support.

DEDICATION

This dissertation is dedicated to my late grandfather Mr Phuti Thomas Semenya.

ABSTRACT

Wings of birds differ significantly in relation to their flight mode, life-history, and habitat. Most seabirds have high aspect ratio wings for efficient gliding, whereas those that dive tend to have shorter wings with lower aspect ratio. Some seabirds including petrels, auks and, to a lesser extent, gannets use their wings to ‘fly’ underwater as well as in the air. These different environments differ greatly in terms of density. The aim of this study is to investigate if there are differences in the flight feathers of seabirds that use their wings for both underwater and aerial propulsion and seabirds that only use their wings in air. The study was restricted to the order Procellariiformes because of the wide range of divers and non-divers. I sampled 33 species ranging from albatrosses to diving petrels, including species that can dive quite well and those that barely dive at all. Due to the 800-fold difference in density between water and air, I expected to find structural differences in the flight feathers of petrels that use their wings underwater and those that do not. The investigation was based on feather length, mass, micro-structure and stiffness relative to body mass. I expected the feathers of birds that dive well (those that attain depths more than 10 m deep) to be shorter (derived from their short wings), heavier, and stiffer compared to the feathers of birds that seldom dive. Further, I expected the differences to be more marked in the primaries compared to the secondaries, because primary feathers are subject to greater forces during flight. Allometric comparisons showed both expected and unexpected results. The primary feathers of diving birds were shorter relative to body mass while the secondaries showed no differences between the two groups. As a result, non-diving birds had heavier primaries compared to the diving birds while there was no difference in the secondaries. As expected, diving birds had heavier feathers relative to feather length. There were minimal to no differences in feather microstructure or stiffness between divers and non-divers. However, diving birds exhibited slightly less flexure relative to the length of their flight feathers than non-diving birds, suggesting that their feathers are slightly stiffer. Diving birds appear to have adapted to utilising the two contrasting media by evolving short, slightly heavy and stiff outer primaries, but these differences are not marked. The main adaptation to flight underwater probably is to partly close the wing, reducing its area and increasing the overlap between adjacent feathers.

CHAPTER 1: GENERAL INTRODUCTION

Flight has only evolved a handful of times, and among the most successful exponents of flight are birds (Maina 2000; Scott and McFarland 2010). The ancestors of modern birds may have evolved flight to avoid predation or aid in prey capture (Fedduccia 1995; 1996; Hedenström 2002), but it has made them the most successful group of terrestrial vertebrates in terms of species richness (Owens *et al.* 1999). The ability to fly also has made birds the most mobile organisms on earth, and they use this mobility to exploit remote or seasonal resources (Hedenström 2002). However, these advantages come at a cost. Flight is energetically expensive due to the low density of air (Pennycuick 1987b), and therefore requires the evolution of a suite of structural adaptations. These include various weight-saving adaptations (e.g. pneumatized bones, pterylae tracts, fusion of skeletal elements, and lack of teeth), but the single most important structural adaptation for flight was the development of feathered wings (Welty 1955; Schwilch *et al*. 2002; Currey 2003; Dumont 2010). Bird wings are adapted from forelimbs, with their surface area greatly increased by a series of overlapping feathers. The evolution of wings largely prevented the use of the forelimbs for other functions, which, together with the need for a light-weight body, greatly constrains the avian body plan (Brusatte *et al.* 2014).

FEATHER STRUCTURE

Feathers are complex keratinous scales (Prum and Williamson 2001; Scott and McFarland 2010; Longrich *et al*. 2012) that have evolved different anatomies for specific functions (Harvey *et al*. 2013). These functions include insulation (Whittow 1986; Swanson 1991; Wolf and Walsberg 2000), protection, camouflage and signalling (Höglund 1964; Lindstom and Nilsson 1988; Møller *et al*. 2006), and other specialised functions restricted to a few species such as water transport (in breeding male sandgrouse), and sound production (Stettenheim 1976). The main flight feathers of the wing are the 10 (sometimes 9-11) primary feathers attached to the bird's 'hand' that are mainly used for propulsion. The secondary feathers, attached to the forearm, provide lift during flight (Newton and Marquiss 1982). The number of secondaries depends on bird size and wing shape; larger birds generally have more secondaries, and birds with long, thin wings typically have more secondaries than birds with short, broad wings (Bostwick *et al.* 2002).

Like all feathers, flight feathers are built from keratin, synthesized in a collar (Lucas and Stettenheim 1972; Prum 1999), and have the same basic building blocks as contour feathers: a calamus, rachis, and a vane comprised of interlocking barbs and barbules (Figure 1.1). Flight feathers have a stiff rachis, which extends from the calamus, the base of the feather that is firmly held in the follicle in the bird's skin. On both sides of the rachis are extensions called barbs forming a vane (Scott and McFarland 2010; Harvey *et al.* 2013). Slender filaments called barbules on each of these barbs extend from the rami (shaft of the barb), and they in turn bear barbicels (Dyck 1985; Johnsgard 1993; Stettenheim 2000). The barbicels hook the barbules together, thereby maintaining the shape of the feather (Bartels 2003). During extreme aerodynamic forces, fighting or collisions with hard objects, the hooks holding the barbs together may be pulled apart; the bird can simply re-attach them using its bill during preening (Nachtigall 1974).

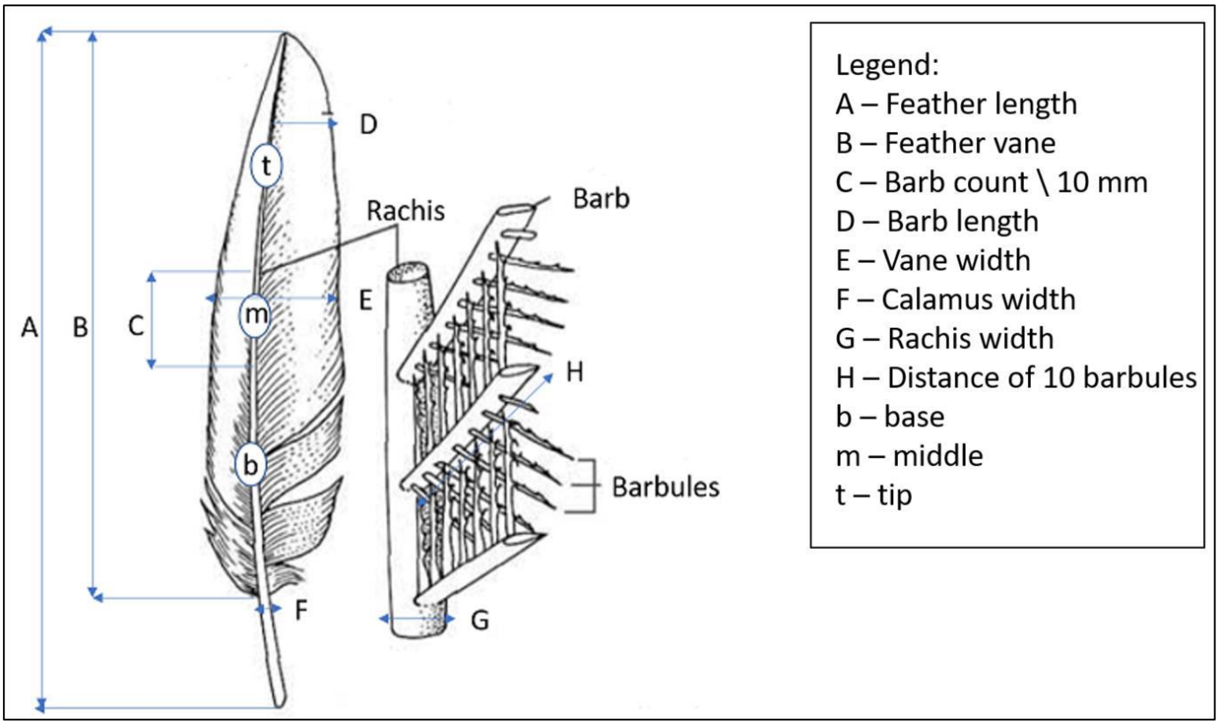


Figure 1.1. The structure of a pennaceous feather (adapted from Cecile Duray-Bito, courtesy of Google images).

Differences in flight feather morphology are influenced by aerodynamic forces, wing loading (Broggi *et al*. 2011) and the varied media to which they may be subjected. Flight feathers of birds face considerable forces and loadings during flight. These forces are greater on the outer than on the inner primaries, and on the tips and middle rather than the feather base (Ennos *et al.* 1995). The bases of both primaries and secondaries are shielded by coverts; therefore, the middle and tips of flight feathers can withstand out-ofplane forces better than the bases (Murphy 1936; Ennos 1995). However, to achieve good aerodynamic performance, the flexural stiffness of the feather rachis (Worcester 1996; Wang *et al*, 2012) must be adapted to avoid excessive bending or breakage (Corning and Biewener 1998).

WINGS FOR DIFFERENT OCCASIONS

The shapes of bird wings vary tremendously among species as a result of their different flight modes (Murphy 1936; Warham 1977; Scott and McFarland 2010), linked to their exploitation of different habitats (Pap *et al*. 2015). Species that occur in dense vegetation tend to have rounded wings with a low aspect ratio (wing- span/mean chord), whereas fast aerial species and soaring birds that do not have to execute tight turns have long, pointed wings and high aspect ratios (Hamilton 1961; Rayner 1988; Lockwood *et al*. 1998). Wing shapes are largely determined by the relative lengths of the primary feathers and the number of secondary feathers. Primary feathers of pointed wings increase markedly in length from the inner to the outermost one, whereas primaries of rounded wings are more even in length (Dawson 2005).

Wing sizes of seabirds vary tremendously relative to body size (Figure 1.2), but with a few exceptions, the shape of their wings does not vary much (Pennycuick 1987a). Most have long, pointed wings for efficient gliding and soaring (Warham 1977). Penguins, which have lost the power of flight entirely, have short, stiff flippers for ‘flying’ underwater (Hui 1988; Bannasch 1994). The extinct Great Auk *Pinguinus impennis* (Houston *et al.* 2010) also was flightless, with a heavy body and short wings. However, the extant auks can still fly. They have relatively short wings, which are used for both aerial and underwater flight (Pennycuick 1987b). However, diving in pursuit of prey comes with problems of buoyancy. Buoyancy is largely dependent on the volume of air found in the respiratory system and the bird’s feathers (Stephenson *et al*. 1989). As a bird dives to increasing depths, the air trapped in plumage is compressed, reducing its buoyancy and hence, beyond a certain depth, the bird becomes negatively buoyant (Wilson *et al*. 1992). This also reduces the bird’s insulation (Wilson *et al*. 1992) but this may be compensated by denser plumage (Tregear 1965).

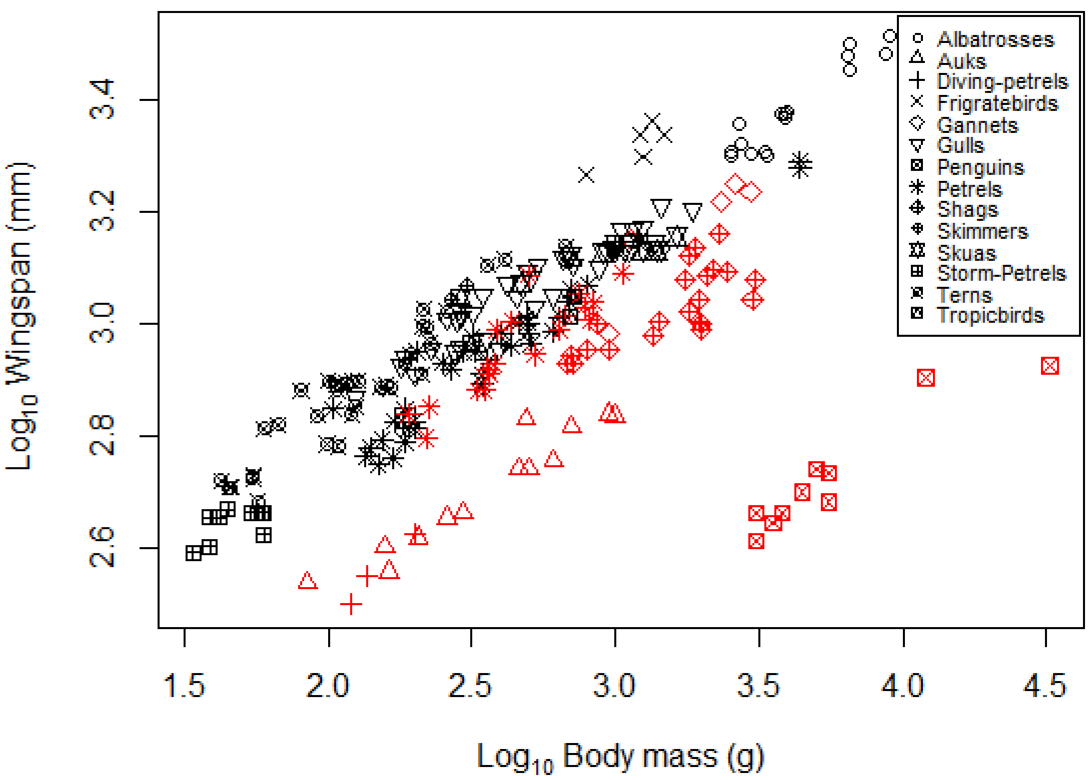


Figure 1.2: Seabird wingspans relative to body mass. Red symbols show species that regularly dive > 10 m while black symbols are species that either dive < 10 m or do not dive at all (Marchant and Higgins 1990; Del Hoyo *et al*. 1992; Hockey *et al*. 2005).

Most birds only use their wings for aerial flight, but some birds that feed underwater also use their wings underwater. They face a challenge because the two contrasting media, air and water, have very different densities, and thus the two media select for different traits (Denny 1993). Aquatic birds have evolved three diving adaptations:

1. Foot-propelled divers (Lovvorn 1991; Lovvorn and Jones 1994) have large webbed feet that are shifted towards the birds' tail, compromising locomotion on land (e.g. cormorants, ducks, grebes, divers/loons).
2. Momentum divers (Viosin 1981; Viosin 1982; Garthe *et al.* 2000; Ropert-Coudert *et al.* 2004; Garthe *et al.* 2007) use momentum generated in flight to penetrate water by diving from the air (e.g. gannets, boobies, tropicbirds, terns).

3. Wing-propelled divers (Pennycuick 1987b; Kooyman 1989; Lovvorn *et al.* 2001) use their wings to 'fly' underwater. The much greater density of water than air is especially acute for these birds; some species have entirely adapted to flight underwater losing the ability to fly in air (e.g. penguins, Great Auk), whereas others strike a compromise that allows flight in both media (e.g. auks, diving petrels, shearwaters and some other petrels).

Most seabird families have a single main foraging mode; all the auks are wing- propelled divers, all the cormorants are foot-propelled divers. Only the Procellariidae (petrels, shearwaters, allies) exhibit a diversity of foraging behaviours and associated flight patterns (Pinaud and Weimerskirch 2006). They are the largest family within the order Procellariiformes, which ranges in size from the tiny storm petrels (Hydrobatidae and Oceanitidae, 30 g) to albatrosses (Diomedeidae, up to 10 000 g; Warham 1977, Figure 1.3). The storm petrels have relatively long, broad wings with a fairly low aspect ratio and very low wing loading that allows them to skip along slowly, picking prey from water surface (Warham 1977). The albatrosses have long narrow wings, with the highest aspect ratios of any bird, and are adapted for dynamic soaring, travelling vast distances with little energy expenditure (Sato *et al*. 2009). The petrels and shearwaters lie between these two extremes, and contain birds with a wide range of diving abilities. Some petrels are poor divers (e.g. fulmarine and gladfly petrels; Kovacs and Meyer 2000), whereas other, notably many shearwaters, are proficient wing-propelled divers, attaining depths of up to 70 m underwater (Weimerskirch and Sagar 1996; Shaffer *et al.* 2006). Even within the shearwaters, however, there is a range of diving abilities from the large, warm-water *Calonectris* species, which have large wings for efficient gliding, to the smaller *Ardenna* and *Puffinus* species which have shorter wings and higher wings loadings (Kuroda 1954; Warham 1977, 1990). The diving petrels are most specialised, closely resembling small auks – their northern hemisphere ecological analogues – and fly underwater extremely well (Figure 1.2). They possess short wings with a medium- low aspect ratio and high wing loading, resulting in very fast, laboured flight in air (Murphy 1936). Their morphology is so distinctive that they were originally placed in a separate family, the Pelecanoididae, but genetic studies show they are only highly modified petrels (Barrowclough *et al*. 1981; Viot *et al*. 1993).

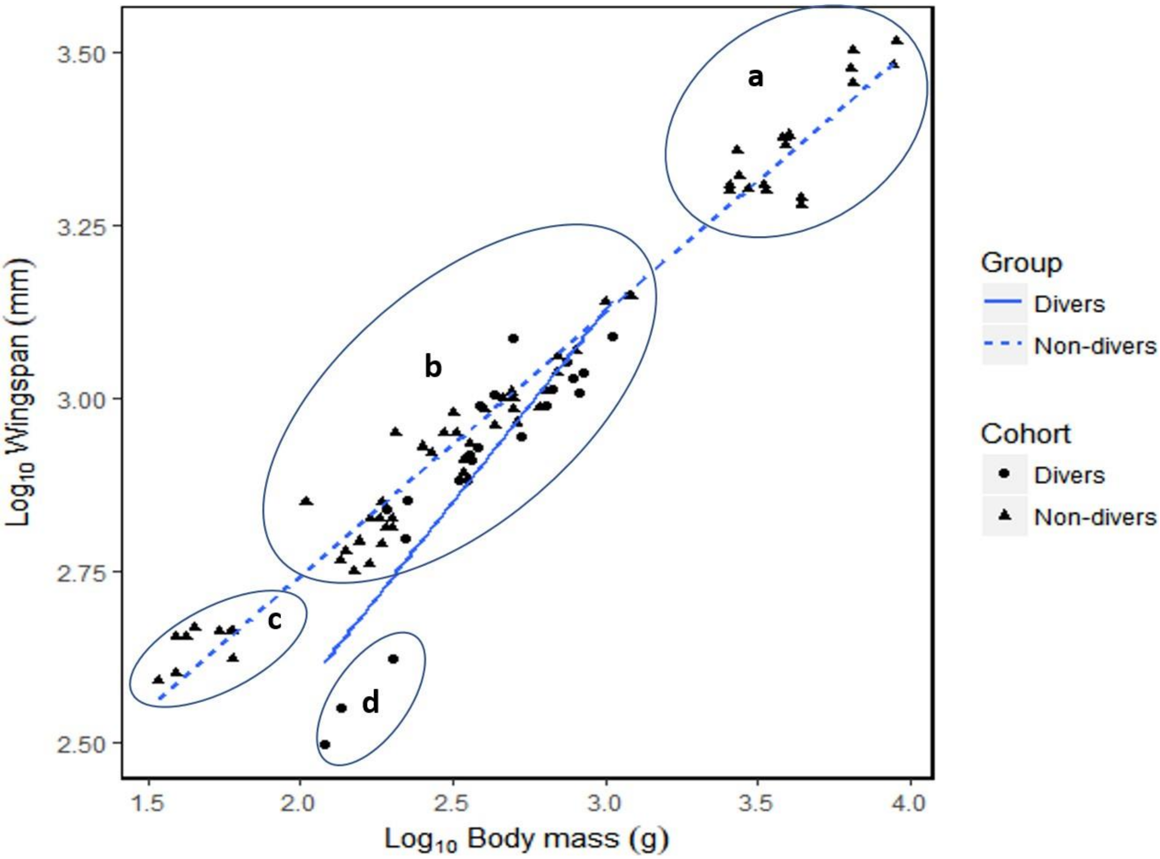


Figure 1.3: Wingspan of Procellariiformes (a - albatrosses, b – petrels, c – storm petrels and d – diving petrels) relative to body mass. Diving petrels (d) deviate from the rest of the petrels by having short wings relative to their bodies. The regression lines show how petrels that routinely dive differ from the rest of the petrels.

REQUIREMENTS FOR AERIAL AND UNDERWATER FLIGHT

Birds that employ both aerial and underwater flight face several key challenges (drag, buoyancy, inertia and gravity), and have had to trade-off various physiological, morphological and behavioural adaptations to live in the two media (Kendeigh *et al*. 1977; Whittow and Rahn 1984). Small wings allow wing-propelled birds to flap effectively underwater (Wilson *et al*. 1992), but increase flight costs in the air (Pennycuick 1987a). In general, like marine mammals, large seabirds can dive more deeply because they have larger oxygen stores and lower mass-specific metabolic rates than small seabirds (Figure 1.4, Welty 1955). However, among birds that fly in both air and water, birds with short wings relative to their body size dive deeper than birds with long wings (Pennycuick 1987a). Diving depth is highly influenced by body mass, all other birds seem to dive deeper with increased body size except for petrels and albatrosses.

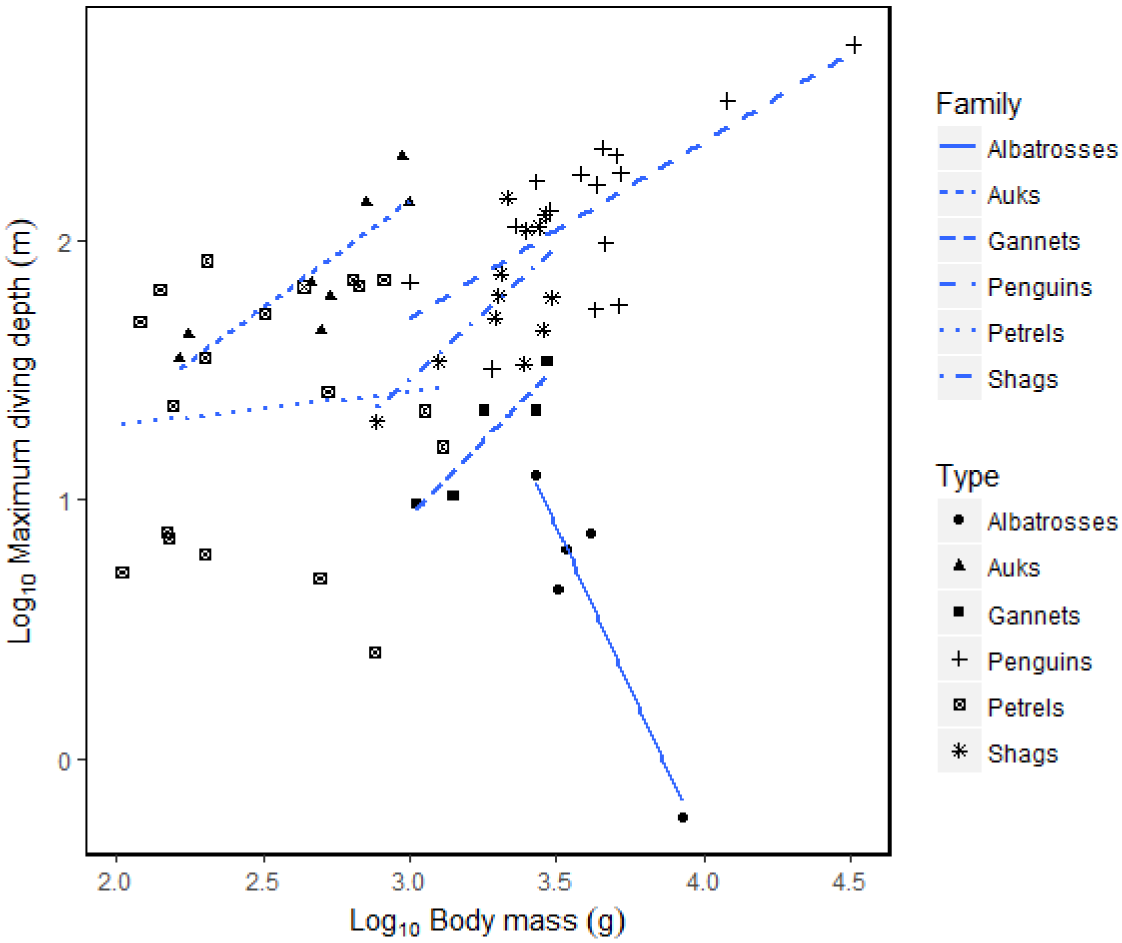


Figure 1.4: Maximum diving depth of seabirds relative to body mass (from data in Ropert-Coudert and Kato 2012). The regression lines show that the penguins have the largest body masses and dive deepest, however, they only use ‘fly’ in water, not in air. The petrels show no significant relationship between dive depth and body size due in large part to the bimodal distribution of dive depths within this group.

STUDY ORDER

The order Procellariiformes comprises 144 species of seabirds in four families: Diomedeidae (albatrosses, 21 species), Hydrobatidae (northern storm petrels, 17 species), Oceanitidae (southern storm petrels, nine species) and Procellariidae (petrels, diving petrels, prions and shearwaters, 96 species). They vary greatly in size, from 0.03 kg storm petrels to 10 kg albatrosses. The Procellariidae have almost as large a body size range, from 0.1 kg Bulwer’s Petrel *Bulweria bulwerii* to 3.2 kg giant petrels

Macronectes spp. Most species are largely aerial, spending much of their time scouring the sea for food, and feeding within a metre or so of the sea surface. However, some species of petrels are proficient divers, reaching depths of up to 70 m in pursuit of prey (Table 1.1). All species feed mainly on cephalopods, fish and small marine invertebrates; some larger species may also feed on other birds. They are found across all oceans and mostly breed in colonies on offshore islands where there are no terrestrial predators, but a few species breed on coastal cliffs and in inland deserts that are largely predator-free. They are characterized by a hooked bill, covered in horny plates and have raised tubular nostrils. Penguins are their closest relatives (Prum *et al*. 2015).

Table 1.1: The diving ability of Procellariiformes, based on data from Penguiness website (Ropert-Coudert and Kato 2012). Asterisks denote genera that have been recorded to dive > 10 m deep.

Family	Genus	Number of species	Body mass (g)	Maximum diving depth (m)
Oceanitidae				
	Oceanites	3	34-45	< 2
	Garrodia	1	34	< 2
	Pelagodroma	1	60	< 2
	Fregetta	3	50-60	< 2
	Nesofregetta	1	~60	< 2
Diomedeidae				
	Phoebastria	4	2300-3600	< 10
	Diomedea	6	4800-11300	< 2
	*Phoebetria**	2	2400-3100	12
	Thalassarche	9	2400-5000	< 8
Hydrobatidae				
	Hydrobates	1	23-29	< 2
	Oceanodroma	17	29-59	< 2
Procellariidae				
	Macronectes	2	3800-5000	< 2
	Fulmarus	2	700-835	< 10
	Thalassoica	1	510-765	< 10
	Daption	1	340-380	< 10
	Pagodroma	1	240-460	< 10
	Halobaena	1	170-230	< 10
	Pachyptila	6	90-235	< 10
	Aphrodroma	1	331-357	< 10
	Pterodroma	35	140-810	< 10
	Pseudobulweria	5	160-270	< 10
	*Procellaria**	5	680-1420	20
	Calonectris	4	440-956	< 10
	*Ardenna**	7	300-978	70

*Puffinus**	21	150-525	30
*Pelecanoides**	4	86-185	70
Bulweria	3	78-130	< 10

The physiology of wing-propelled, foot-propelled and plunge divers has been studied quite extensively (Wilson *et* al. 1992; Lovvorn and Jones 1994; Lovvorn *et al*. 2001), but only a few studies have focused on whether their feathers have distinct structural adaptations for underwater flight (Pap *et al*. 2015; 2016). In this thesis I test whether there are structural differences in the flight feathers of Procellariiformes that use their wings for aerial and underwater flight, such as the shearwaters and diving petrels, comparing them to related species that mainly use their wings for aerial flight as a control. Based on the much greater density of water than air, I expect the feathers of divers to be shorter than those of non-divers. I predict that birds that regularly use their wings for underwater propulsion as well as aerial flight should have flight feathers with increased structural strength relative to closely related species that seldom if ever 'fly' underwater to cope with the greater density of water. I further predict that this effect will be most marked among the outer primaries, which bear the greatest forces during flight in either medium than the inner primaries and secondaries.

OUTLINE OF THE THESIS

This project was designed to understand the feather adaptations of aerial seabirds that also use their wings for underwater 'flight'. Chapter 2 focuses on the relationship between the length and mass of flight feathers relative to body mass. Body organs grow relative to body mass, this has been studied greatly through allometric scaling relatonships; therefore, allometric scaling between feather length and body mass is used to help understand how diving species achieve short wings. The scaling between feather length and feather mass (feather mass grow three times over (cubic), by length, width and depth) shows how diving birds have invested in their feathers to be able to use their wings in different media. Further, this chapter compares the ultra-structure of the flight feathers between petrels that use their wings for both the aerial flight and underwater flight with those that use their wings for aerial flight only. Chapter 3 focuses on the rachis depth and stiffness relative to feather length and body mass. These relationships will provide a better understanding of the feather mechanical properties of the diving verses non-diving birds. This will help better understand how the divers have adapted to use their wings in two strongly contrasting media.

CHAPTER 2: HOW DOES UNDERWATER FLIGHT INFLUENCE THE SIZE AND MASS OF PROCELLARIFORM FLIGHT FEATHERS?

ABSTRACT

Amongst other functions of feathers, some birds use their wings for underwater propulsion. This chapter investigates if there are differences between the flight feathers (primaries and secondaries) of birds that 'fly' in air and water. Because water is 800 times denser than air, I expect birds that use their wings to 'fly' underwater to have shorter but stronger wing feathers than birds of a similar size that do not dive. This should be reflected by relatively shorter feathers that are heavier per unit length. The study was restricted to the Procellariiformes because this order contains birds that are excellent at diving and those that do not dive at all. Flight feathers from 33 species of albatrosses and petrels were measured and weighed to investigate their scaling relationship relative to their body mass. Standardised major axis regressions (model II) were used to analyse the allometric relationships of feather length and mass as well as feather length relative to feather mass. As expected, the feathers of wing-propelled diving birds were shorter, particularly in the smallest diving birds; only minor differences were found in the larger petrels that use their wings for underwater propulsion. There was no relationship between body mass and feather mass, presumably because the two predictions (for diving species to have shorter but stronger feathers) contradict each other. The microstructure showed unexpected results; there were minimal to no differences between the diving and non-diving birds. The absence of very large petrels that are efficient divers might reflect a physical constraint on the upper limit of wings that can function effectively in air and water.

INTRODUCTION

What is a long feather or a short feather? What is a heavy feather or a light feather? These questions can only be answered by taking account of the body size of the bird in question. Allometric studies assess how shapes, sizes, physiology and behaviour scale with body mass (West *et al.* 1997; Damuth 2001). For instance, large animals have a lower mass-specific metabolic rate (Peters 1983; Schmidt-Nielsen 1984; Enquist *et al*. 1998; Bettencourt *et al*. 2007) than small animals. A comprehensive understanding of the functional morphology of an organism is impacted by its size (McMahon 1975; Peters 1983; Schmidt-Nielsen 1984; Labarbera 1989; Bertram and

Biewerner 1990) and scaling outcomes (Robinson and Motta 2002). However, assessing only one part (e.g. size of head) of the organism without taking into account the size or mass of the organism would not answer the questions of how it is confirmed that a feather is long or short, heavy or light. The allometric equation used to scale parameters against body mass is:

$$Y = aM^b$$

where, Y is the investigated parameter, *a* is the allometric coefficient or the intercept constant (Howland *et al.* 2004), M is the body mass and b is the regression slope. This can be represented as a linear relationship by log-transforming the data:

$$\text{Log}(y) = \text{Log}(a) + b\text{Log}(M_b)$$

If the slope b>1.0, allometry is positive (e.g. adhesive pads used for climbing occupy a big surface area on larger animals; Labonte *et al* 2016) and if b<1.0, negative allometry results (e.g. the blood volume of the organism does not increase as fast as body size). If the slope is 1, the relationship is isometric, independent of mass (Schmidt-Nielsen 1984).

Ornithologists have studied variation in wing shapes of birds in relation to flight mode and habitat use (Pennycuick 1987a; Pap *et al*. 2015). However, there is little knowledge on how feathers vary across different flight modes and habitat use (see Pap *et al*. 2015). Moreover, flight feathers must be evolved in a way to suit the behaviour and physiological needs of the bird. The quality (length and mass) of feathers are assumed to be determined by body size (Jungers *et al*. 1995). Although most birds only fly in air, some species also use their wings for underwater 'flight'. Pap *et al.* (2015) and (2016) investigated structural differences in two primary flight feathers (P1 and P8) and body feathers from 137 species of birds that use their wings for different flight modes and in different environments. They concluded that aquatic birds have denser feathers compared to other birds, and that the differences were more marked in species that use their wings for underwater propulsion than those that do not.

Seabird wings tend to be fairly uniform in terms of shape (Chapter 1), but the wing-propelled divers deviate from the 'standard seabird' wing shape, having reduced wing span and wing area compared to typical Procellariiformes when controlling for body mass (Pennycuick 1987b, Chapter 1). The small wings of diving petrels are considered a pre-requisite for underwater flight, corroborated by the greatly reduced wing size in penguins (Clark and Bemis 1979). To compensate for the much greater density of water than air, seabirds that use their wings for underwater propulsion bend the wrist and elbow to reduce wing area (Kuroda 1954), and reduce flapping frequency in water (Pennycuick 1987b). As a consequence of their reduced wing areas (and concomitant greater wing loading), wing-propelled divers such as diving petrels and auks seldom glide when flying in air; typically flapping continually (Pennycuick 1987b). Moreover, the bent wing has the same total length, however, the tip of the wing is closer to the body. This reduces the arc through which the wing must move compared to the fully extended wing when flying in air.

Most studies of flight feather allometry to date have focused on the primaries (Dawson 2005; Butler *et al*. 2008; Pap *et al.* 2015), which are less variable in number than the secondaries. Most birds have ten primaries (occasionally 9-11), but the number of secondaries varies from 10 to 40 just within the Procellariiformes, determined by body size and wing length (Figure 2.1, Table 2.1). In this chapter I compare feather length to body mass, feather mass to body mass and feather mass to feather length of both the primary and secondary feathers, to determine whether there are differences between specialist diving species and non-diving species of procellariiform birds. I test whether the flight feathers of wing-propelled diving species are relatively shorter and heavier (to confer greater structural strength) given that the density of water is 800 times more than the air. I use allometric scaling to determine the relationships between feather length and mass and body mass. I predict that, 1) wing-propelled divers should have shorter feathers relative to their size (body mass), and 2) the primary feathers of the wing-propellers should be relatively heavier because they are faced with greater most of the aero/hydrodynamic forces than the secondary feathers.

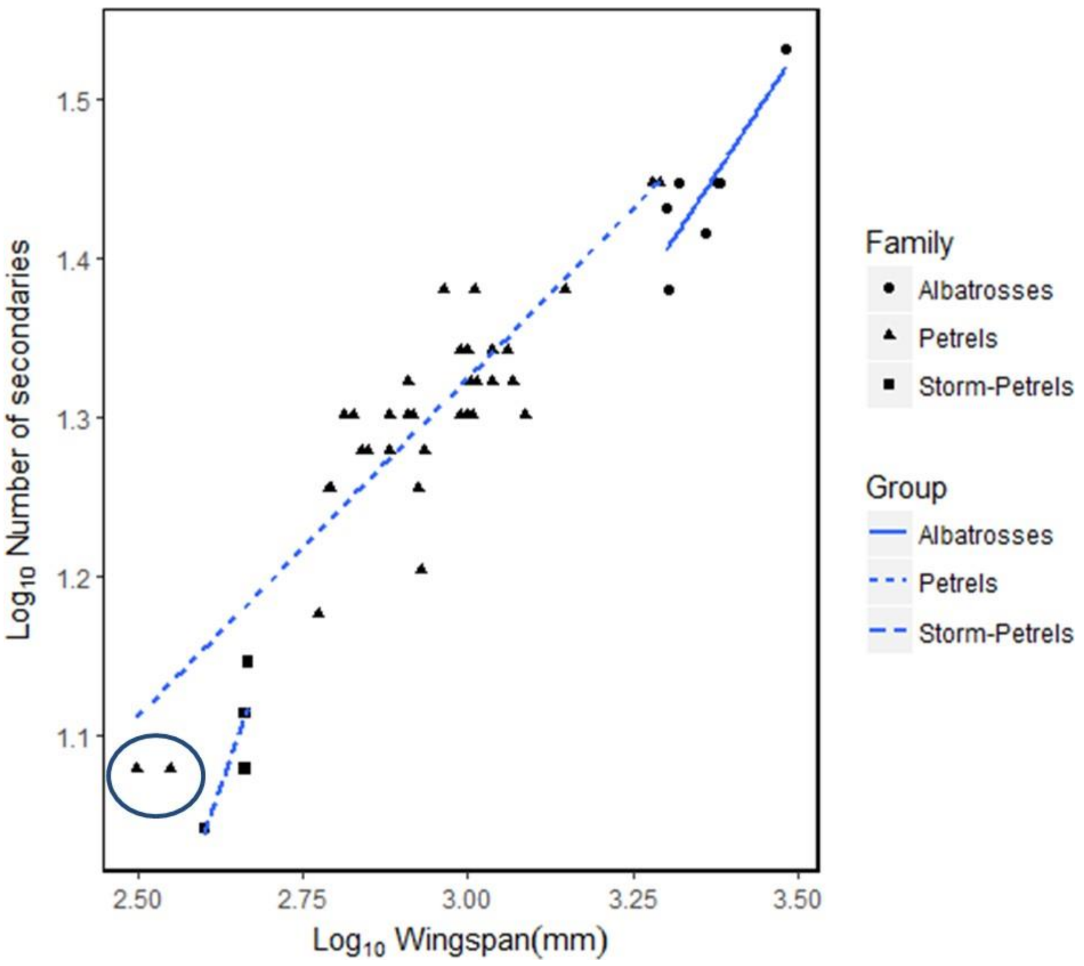


Figure 2.1: The number of secondary feathers relative to wingspan among the Procellariiformes. The circled triangles are the diving petrels (data from Appendix 1).

Table 2.1: The allometric relationships for the number secondary feathers relative to wingspan among different groups of procellariform birds.

Group (sample size)	Slope (95% CI)	Intercept (95% CI)	R^2
Non-divers (24)	0.43 (0.36-0.50)	0.02 (-0.20-0.24)	0.83***
Divers (9)	0.46 (0.37-0.54)	-0.05 (-0.29-0.20)	0.90***
Procellariidae (20)	0.42 (0.35-0.51)	0.05 (-0.19-0.28)	0.77***
Procellariiformes (33)	0.43 (0.38-0.49)	0.01 (-0.15-0.18)	0.85***

*P<0.05 **P<0.01 ***P<0.001

METHODS

Sampling

Primary and secondary flight feathers from a wide diversity species of Procellariiformes were collected from birds found dead (e.g. killed by predatory brown skuas *Catharacta antarctica* or killed accidentally on longlines; Ryan *et* al. 2002; Rollinson *et al*. 2017). The study species include birds that regularly use their wings for flying underwater (diving petrels and some shearwaters), those that seldom use their wings underwater (albatrosses, storm petrels, prions and *Pterodroma* and fulmarine petrels), and species that lie between these extremes (*Procellaria* petrels and some shearwaters). I categorised divers and non-divers according to how deep they dive underwater (see Table 1.1, Chapter 1).

Primaries were sampled from all individuals and secondaries were sampled from all birds with the exception of Sooty Shearwater (Table 2.2). Only feathers that were fully grown and not showing excessive signs of wear were measured for all the parameters; birds in active primary moult were not sampled. The feathers were plucked, dried in an oven at 30°C for 48 hours. The length of each feather was measured to the nearest 1 mm from the base of the calamus to the end of the vane using a stopped wing ruler. Each feather was flattened with the ventral side faced down, to ensure consistent measurements. Mass was recorded to the nearest 0.1 mg (1 mg for feathers weighing > 1 g) on an A&D GH-202 balance. It was seldom possible to measure the body mass of the birds from which the feathers were collected because of the way they died, so I assumed average body masses from Hockey *et al.* (2005) and Marchant and Higgins (1990).

I also examined feather micro-structure by measuring the following parameters:

a. barb length;

b. vane width to the nearest 0.1 mm with Vernier callipers.

c. In addition, barb density was estimated by counting the number per 10 mm section along the rachis using a dissecting microscope. Barbule density was estimated by measuring the length of barb (μm) supporting ten barbules using ImageJ software (Schneider *et al*. 2012), and the distance converted to density (n per mm) using the equation: 1000/(distance/9) because there are nine gaps between 10 adjacent barbules. Both density estimates were made on the inner web (trailing edge, Ennos *et al*. 1995) of the feather vane at the same locations as the measurements (tip, middle and base).

All these measurements were taken at three points on each feathers: tip (75% of the way from the base of the vane to the tip), middle (50%) and base (25%; Figure 1.1).

Table 2.2: The 33 species of Procellariiformes that this study was based on, and the numbers of individuals for which sets of primaries and secondaries were available.

Common name	**Species name**	**Primaries**	**Secondaries**
Common Diving-Petrel	*Pelecanoides urinatrix**	2	2
South Georgian Diving-Petrel	*Pelecanoides georgicus **	5	1
White-chinned Petrel	*Procellaria aequinoctialis**	10	5
Spectacled Petrel	*Procellaria conspicillata**	1	1
Grey Petrel	*Procellaria cinerea**	4	4
Great Shearwater	*Ardenna gravis**	4	6
Little Shearwater	*Puffinus assimilis**	7	7
Hutton's Shearwater	*Puffinus huttoni**	1	1
Sooty Shearwater	*Ardenna grisea**	1	0
Blue Petrel	*Halobaena caerulea**	24	4
Broad-billed Prion	*Pachyptila vittata**	21	23
Fairy Prion	*Pachyptila turtur**	5	5
Kerguelen Petrel	*Lugensa Brevirostris**	4	2
Atlantic Petrel	*Pterodroma incerta**	6	8
Soft-plumaged Petrel	*Pterodroma mollis**	12	13
Great-winged Petrel	*Pterodroma macroptera**	2	2
White-Headed Petrel	*Pterodroma lessonii**	1	1
Pintado Petrel	*Daption capense **	1	1
Southern Giant Petrel	*Macronectes giganteus**	5	3
Salvin's Prion	*Pachytila salvini**	6	1
White-bellied Storm Petrel	*Fregetta grallaria*	7	8
Black-bellied Storm Petrel	*Fregetta tropica*	2	2
White-faced Storm Petrel	*Pelegodroma marina*	11	10
Grey-backed Storm Petrel	*Garrodia nereis*	1	1
Leach's Storm Petrel	*Oceanodroma leucorhoa*	1	1
Atlantic Yellow-nosed Albatross	*Thalassarche chlororhynchos*	1	1
Black-browed Albatross	*Thalassarche melanophris*	8	7
Indian yellow-nosed Albatross	*Thalassarche carteri*	4	3
Shy Albatross	*Thalassarche cauta*	6	5
Grey-headed Albatross	*Thalasarche chrysostoma*	8	8
Sooty Albatross	*Phoebetria fusca*	1	1
Tristan Albatross	*Diomedea dabbenena*	1	1
Wandering Albatross	*Diomedea exulans*	3	2

*Represents the Procellariidae family.

Statistical analyses

I used reduced major axis (model II) regressions to assess allometric relationships, because this model does not have dependent and independent variables and takes account of errors in both the x-and-y axes (Ricker 1973; McArdle 1988). I summed the lengths and masses of the feathers across all the primaries and secondaries for each individual bird, and used the average value for each species in regressions among species. Given considerable variation in sample size among species, I used the jack-knife method to assess whether particular species strongly influenced the allometric regression parameters (Jones 1974; Bissell 1977) and the jack-knifing did not change the results. The jack-knife method of investigating and reducing the bias in nonlinear estimates of parameters is applied to stratified samples from a multivariate population of limited size. I also explored patterns within individual feathers to test whether the outer feathers showed a stronger signal of the diving effect than the inner primaries and secondaries. I fitted estimated slope and intercept with associated 95% confidence intervals, coefficient of determination (R^2) and the significance of the regression (p-value) using the statistical environment R (R Core Team 2017, Logan 2010). I further used analysis of covariance (ANCOVA) test to compare slopes between the diving and non-diving birds.

RESULTS

The study was based on primaries from 176 birds and secondaries from 140 birds from 33 species of albatrosses and petrels (Table 1.1, Table 2.2, Appendix 1).

Feather length relative to body mass

As expected, there was a strong correlation between body mass and total length of flight feathers (primaries and secondaries combined). Species that regularly dive > 10 m tended to have shorter feathers relative to their body mass (Figures 2.2-2.4). Length typically scales with mass with a slope of 0.33, so primary feather length is negatively allometric in Procellariiformes overall, and among non-diving petrels (Table 2.3). However, primary length in petrels that dive is positively allometric, and the overall relationship for the Procellariidae is not significantly different from isometry (Table 2.3). The length of secondary feathers is positively allometric for all groups (Table 2.3) because the number of secondaries increases with body size (Figure 2.1). However, the relationship is stronger for divers than for non-divers, which shows that as body size increases, divers increase secondary feather length (a proxy for wing area) faster than the non- divers. However, the difference in allometry between divers and non-divers is greater for primaries than secondaries (Table 2.3). Overall, the total length of all flight feathers tends to be positively allometric due to the increasing number of secondaries (Table 2.3), but again the signal is much stronger among petrels that dive, and in the case of non-diving petrels, the 95% confidence interval includes isometry.

Table 2.3: The allometric relationships between average total feather length and body mass among various groups of procellariform seabirds. 'Non-divers' include all petrels (Procellariidae) that dive to < 10 m (11 species); divers are Procellariidae that dive > 10 m (nine species). Regression parameters are given with 95% confidence intervals (CI).

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Total	Non-divers	0.35 (0.33-0.37)	2.63 (2.57-2.68)	0.98***
	Divers	0.53 (0.46-0.60)	2.04 (1.85-2.23)	0.98***
	Procellariidae	0.41 (0.33-0.40)	2.42 (2.20-2.65)	0.85***
	Procellariiformes	0.37 (0.33-0.40)	2.50 (2.46-2.65)	0.94***
Primaries	Non-divers	0.24 (0.23-0.26)	2.59 (2.55-2.64)	0.97***
	Divers	0.43 (0.39-0.47)	2.00 (1.89-2.12)	0.99***
	Procellariidae	0.33 (0.27-0.40)	2.31 (2.13-2.49)	0.85***
	Procellariiformes	0.26 (0.23-0.29)	2.52 (2.43-2.61)	0.90***
Secondaries	Non-divers	0.46 (0.42-0.49)	2.04 (1.94-2.15)	0.97***
	Divers	0.65 (0.53-0.74)	1.48 (1.21-1.75)	0.97***
	Procellariidae	0.48 (0.37-0.59)	1.96 (1.67-2.24)	0.83***
	Procellariiformes	0.48 (0.43-0.52)	1.97 (1.86-2.09)	0.95***

*P<0.05 **P<0.01 ***P<0.001

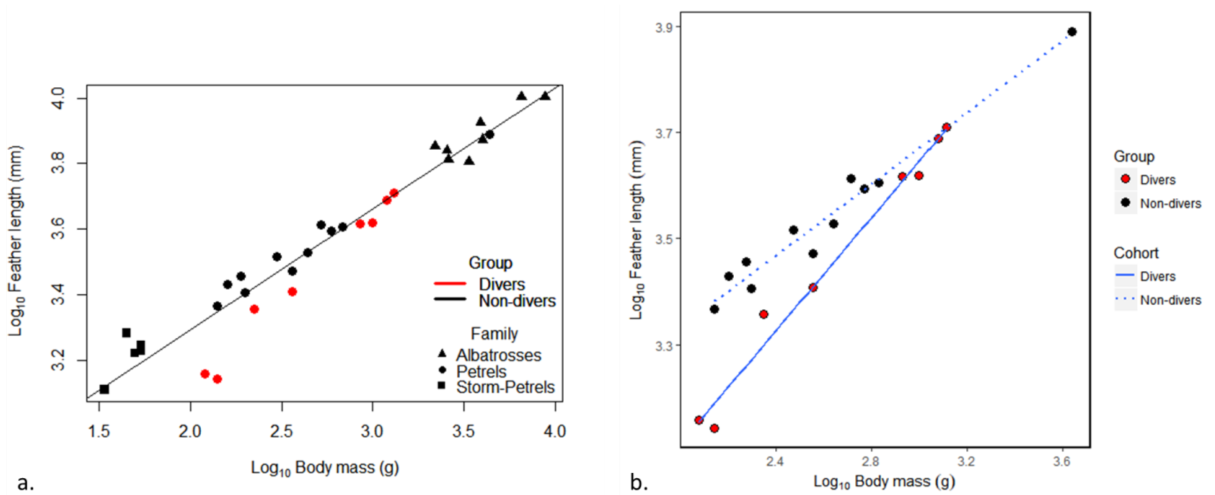


Figure 2.2. The influence of diving behaviour on the relationship between total flight (primary and secondary) feather length and body mass among (a) 33 species of

Procellariiformes (slope: 0.37 (95% CI 0.33-0.37) and intercept: 2.50 (95% CI 2.46-2.65)) and (b) 20 species of Procellariidae (slope: 0.41 (95% CI 0.33-0.40) and intercept: 2.42 (95% CI 2.20-2.65)).

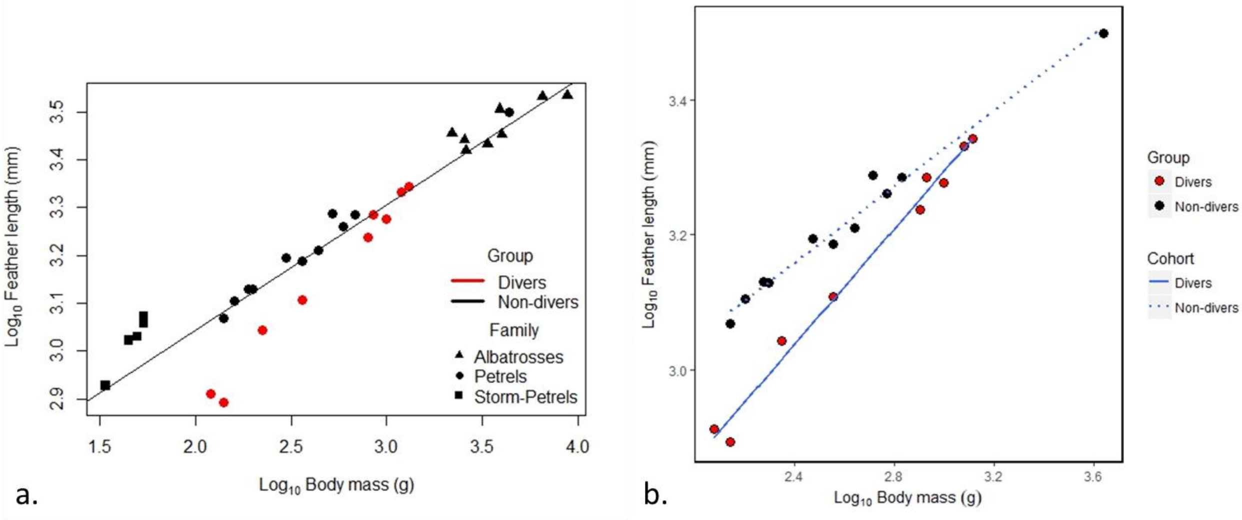


Figure 2.3. The influence of diving behaviour on the relationship between primary feather length and body mass among (a) 33 species of Procellariiformes (slope: 0.26 (95% CI 0.23-0.29) and intercept: 2.52 (95% CI 2.43-2.61)) and (b) 20 species of Procellariidae (slope: 0.33 (95% CI 0.27-0.40) and intercept: 2.31 (95% CI 2.13-2.49)).

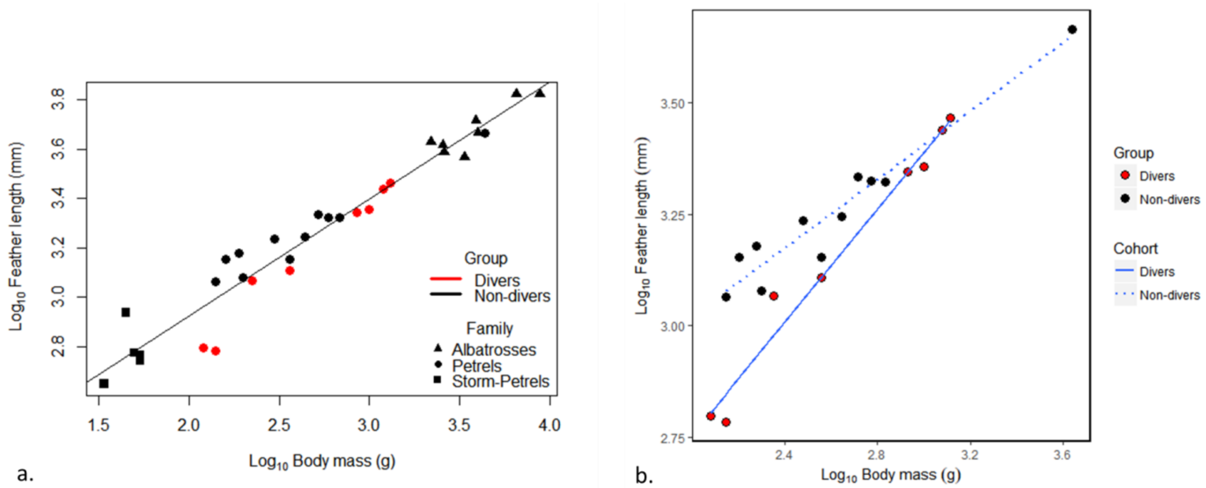


Figure 2.4. The influence of diving behaviour on the relationship between secondary feather length and body mass among (a) 32 species of Procellariiformes (slope: 0.48 (95% CI 0.43-0.52) and intercept: 1.97 (95% CI 1.86-2.09)) and (b) 19 species of Procellariidae (slope: 0.48 (95% CI 0.37-0.59) and intercept: 1.96 (95% CI 1.67-2.24)).

The allometric slopes relating individual primary lengths to body mass showed significant differences between the diving and non-diving birds (Appendix 2) for all feathers except the innermost primaries (Table 2.4). Diving birds showed positive allometry across all primary feathers whereas the family group (Procellariidae) showed positive allometry on the outer primaries except primary ten. Non-divers showed negative allometry with the 95% CI including isometry in most feathers, while the order group (Procellariiformes) showed negative allometry across all primaries. Like the primaries, individual secondary feathers (only ten outer secondaries were used for the individual comparison, because of the differing numbers of secondaries among species) of birds that dive > 10 m showed positive allometry while the non- divers together with all Procellariiformes showed negative allometry (Table 2.5). The Procellariidae overall tended to show negative allometry but some secondaries had 95% CIs including isometry and some had positive allometry. Further, the differences between the individual secondary feathers between the divers and non-divers were found to be significant with the exception of S1 and S2.

Table 2.4: The allometric relationships between primary length and body mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.28 (0.23-0.33)	1.29 (1.15-1.43)	0.93***
	Divers	0.33 (0.29-0.37)	1.09 (0.98-1.21)	0.98***
	Procellariidae	0.29 (0.24-0.34)	1.23 (1.09-1.36)	0.89***
	Procellariiformes	0.24 (0.22-0.27)	1.38 (1.30-1.45)	0.91***
P2	Non-divers	0.28 (0.24-0.33)	1.31 (1.19-1.44)	0.94***
	Divers	0.34 (0.31-0.37)	1.11 (1.03-1.20)	0.99***
	Procellariidae	0.30 (0.25-0.35)	1.25 (1.12-1.38)	0.90***
	Procellariiformes	0.24 (0.21-0.27)	1.43 (1.35-1.50)	0.91***
P3	Non-divers	0.29 (0.24-0.33)	1.35 (1.19-1.44)	0.97***
	Divers	0.37 (0.33-0.40)	1.09 (1.00-1.74)	0.99***
	Procellariidae	0.31 (0.26-0.37)	1.27 (1.12-1.41)	0.89***
	Procellariiformes	0.24 (0.21-0.27)	1.47 (1.40-1.55)	0.91***
P4	Non-divers	0.29 (0.26-0.32)	1.41 (1.33-1.49)	0.98***
	Divers	0.40 (0.36-0.43)	1.05 (0.96-1.15)	0.99***
	Procellariidae	0.32 (0.27-0.39)	0.87 (1.13-1.45)	0.87***
	Procellariiformes	0.25 (0.22-0.28)	1.51 (1.43-1.60)	0.90***
P5	Non-divers	0.29 (0.26-0.33)	1.46 (1.37-1.54)	0.98***
	Divers	0.43 (0.38-0.47)	1.02 (0.91-1.13)	0.99***
	Procellariidae	0.34 (0.27-0.40)	1.30 (1.12-1.48)	0.85***
	Procellariiformes	0.25 (0.22-0.29)	1.34 (1.45-1.63)	0.87***
P6	Non-divers	0.28 (0.24-0.32)	1.53 (1.43-1.63)	0.96***
	Divers	0.45 (0.40-0.49)	0.99 (0.87-1.11)	0.99***
	Procellariidae	0.34 (0.27-0.41)	1.33 (1.13-1.53)	0.83***
	Procellariiformes	0.26 (0.22-0.30)	1.56 (1.46-1.66)	0.88***
P7	Non-divers	0.27 (0.22-0.31)	1.58 (1.47-1.70)	0.95***
	Divers	0.47 (0.41-0.52)	0.97 (0.81-1.12)	0.98***

	Procellariidae	0.34 (0.26-0.42)	1.35 (1.14-1.57)	0.80***
	Procellariiformes	0.27 (0.23-0.30)	1.58 (1.47-1.68)	0.86***
P8	Non-divers	0.29 (0.25-0.32)	1.56 (1.47-1.65)	0.97***
	Divers	0.47 (0.42-0.52)	0.98 (0.85-1.11)	0.99***
	Procellariidae	0.35 (0.27-0.43)	1.35 (1.14-1.56)	0.82***
	Procellariiformes	0.27 (0.23-0.31)	1.59 (1.49-1.70)	0.86***
P9	Non-divers	0.28 (0.24-0.32)	1.59 (1.49-1.68)	0.97***
	Divers	0.48 (0.42-0.53)	0.97 (0.83-1.12)	0.98***
	Procellariidae	0.35 (0.27-0.53)	1.36 (1.15-1.57)	0.82***
	Procellariiformes	0.27 (0.24-0.31)	1.59 (1.48-1.69)	0.87***
P10	Non-divers	0.29 (0.25-0.33)	1.54 (1.44-1.64)	0.97***
	Divers	0.49 (0.42-0.55)	0.93 (0.77-1.10)	0.98***
	Procellariidae	0.31 (0.28-0.44)	1.43 (1.10-1.53)	0.62***
	Procellariiformes	0.29 (0.26-0.33)	1.52 (1.42-1.62)	0.90***

*P<0.05 **P<0.01 ***P<0.001

Table 2.5: The allometric relationships between secondary length and body mass among various groups of procellariform seabirds.

Feather	**Group**	**Slope (95% CI)**	**Intercept (95% CI)**	R^2
S1	Non-divers	0.26 (0.21-0.30)	1.31 (1.20-1.43)	0.94***
	Divers	0.36 (0.29-0.43)	0.97 (0.79-1.15)	0.96***
	Procellariidae	0.30 (0.24-0.35)	1.19 (1.03-1.34)	0.86***
	Procellariiformes	0.25 (0.22-0.27)	1.34 (1.26-1.42)	0.90***
S2	Non-divers	0.24 (0.18-0.29)	1.35 (1.20-1.50)	0.90***
	Divers	0.36 (0.29-0.42)	0.97 (0.79-1.16)	0.96***
	Procellariidae	0.28 (0.22-0.34)	1.21 (1.04-1.38)	0.83***
	Procellariiformes	0.24 (0.21-0.27)	1.35 (1.26-1.43)	0.89***
S3	Non-divers	0.23 (0.17-0.28)	1.37 (1.22-1.53)	0.89***
	Divers	0.35 (0.29-0.42)	0.98 (0.80-1.15)	0.96***
	Procellariidae	0.27 (0.21-0.34)	1.23 (1.05-1.40)	0.81***
	Procellariiformes	0.23 (0.20-0.26)	1.35 (1.27-1.44)	0.89***
S4	Non-divers	0.22 (0.16-0.28)	1.39 (1.23-1.54)	0.88***
	Divers	0.35 (0.28-0.41)	0.99 (0.82-1.16)	0.96***
	Procellariidae	0.27 (0.20-0.33)	1.24 (1.07-1.41)	0.81***
	Procellariiformes	0.24 (0.21-0.26)	1.34 (1.26-1.42)	0.90***
S5	Non-divers	0.22 (0.17-0.28)	1.38 (1.24-1.52)	0.89***
	Divers	0.34 (0.29-0.40)	1.00 (0.85-1.16)	0.97***
	Procellariidae	0.27 (0.21-0.33)	1.24 (1.08-1.40)	0.83***
	Procellariiformes	0.24 (0.21-0.27)	1.33 (1.25-1.41)	0.91***
S6	Non-divers	0.22 (0.17-0.28)	1.38 (1.24-1.52)	0.90***
	Divers	0.35 (0.29-0.41)	0.98 (0.82-1.14)	0.97***
	Procellariidae	0.27 (0.21-0.33)	1.23 (1.07-1.39)	0.83***
	Procellariiformes	0.24 (0.21-0.27)	1.32 (1.24-1.40)	0.91***
S7	Non-divers	0.22 (0.16-0.28)	1.40 (1.25-1.56)	0.87***
	Divers	0.36 (0.29-0.42)	0.97 (0.82-1.14)	0.96***
	Procellariidae	0.27 (0.20-0.33)	1.24 (1.06-1.41)	0.81***

	Procellariiformes	0.25 (0.22-0.28)	1.30 (1.22-1.38)	0.91***
S8	Non-divers	0.22 (0.16-0.27)	1.40 (1.25-1.54)	0.88***
	Divers	0.37 (0.31-0.44)	0.92 (0.75-1.10)	0.96***
	Procellariidae	0.28 (0.21-0.34)	1.22 (1.04-1.40)	0.80***
	Procellariiformes	0.25 (0.22-0.28)	1.29 (1.21-1.37)	0.91***
S9	Non-divers	0.22 (0.16-0.27)	1.40 (1.26-1.54)	0.90***
	Divers	0.38 (0.30-0.46)	0.89 (0.67-1.10)	0.95***
	Procellariidae	0.28 (0.21-0.35)	1.20 (1.01-1.39)	0.79***
	Procellariiformes	0.25 (0.23-0.29)	1.28 (1.19-1.36)	0.91***
S10	Non-divers	0.22 (0.16-0.27)	1.40 (1.26-1.54)	0.89***
	Divers	0.40 (0.31-0.50)	0.83 (0.58-1.09)	0.94***
	Procellariidae	0.29 (0.21-0.37)	1.18 (0.97-1.39)	0.76***
	Procellariiformes	0.28 (0.24-0.31)	1.21-1.12-1.31)	0.90***

*P<0.05 **P<0.01 ***P<0.001

Feather mass relative to body mass

Total flight feather mass also was strongly correlated with body mass but there was no evidence that divers invested greater mass in their flight feathers than non-diving petrels (Table 2.6; Appendix 2). The mass of both primaries and secondaries among Procellariiformes had a negative allometric relationship with body mass. The total mass of flight feathers (Figure 2.5), primaries (Figure 2.6) and secondaries (Figure 2.7) of divers showed positive allometry while the non-diving petrels showed negative allometry. Diving species again fell below the regression line at family and order levels (Figures 2.5-2.7) although not to such a great extent as feather length (Figures 2.2-2.4), suggesting that the reduction in feather length may be driving the relatively low mass of flight feathers (relative to body mass) in diving species.

Table 2.6: The allometric relationships between flight feather mass and body mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95%CI)	R_2
Total	Non-divers	0.84 (0.81-0.89)	1.27 (1.16-1.39)	0.99***
	Divers	1.20 (1.06-1.34)	0.17 (-0.20-0.55)	0.98***
	Procellariidae	0.98 (0.84-1.14)	0.82 (0.42-1.21)	0.91***
	Procellariiformes	0.88 (0.82-0.95)	1.14 (0.96-1.32)	0.96***
Primaries	Non-divers	0.80 (0.70-0.85)	1.23 (1.11-1.35)	0.98***
	Divers	1.18 (1.05-1.30)	0.06 (-0.28-0.39)	0.98***
	Procellariidae	0.96 (0.82-1.11)	0.71 (0.32-1.10)	0.91***
	Procellariiformes	0.84 (0.77-0.91)	1.08 (0.89-1.27)	0.95***
Secondaries	Non-divers	0.95 (0.90-1.01)	0.47 (0.32-0.62)	0.98***

Divers	1.24 (1.09-1.39)	-0.43 (-0.84- -0.14)	0.98***
Procellariidae	1.03 (0.87-1.19)	0.22 (-0.20-0.65)	0.91***
Procellariiformes	0.98 (0.92-1.05)	0.36 (0.18-0.54)	0.97***

*P<0.05 **P<0.01 ***P<0.001

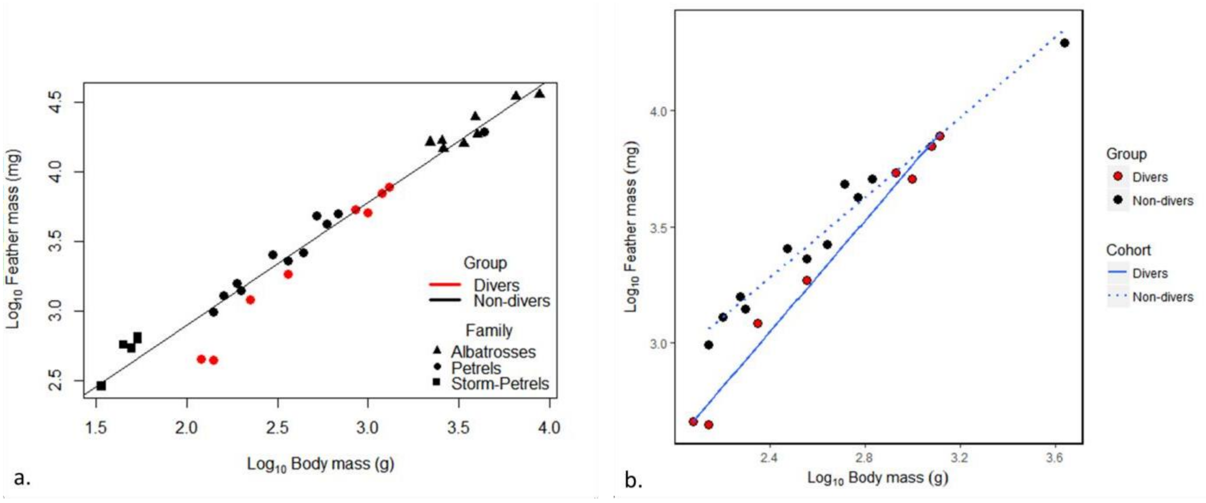


Figure 2.5. The influence of diving behaviour on the relationship between flight feather mass and body mass among (a) 33 species of Procellariiformes (slope: 0.88 (95% CI 0.82-0.95) and intercept: 1.14 (95% CI 0.96-1.32)) and (b) 20 species of Procellariidae (slope: 0.98 (95% CI 0.84-1.14) and intercept: 0.82 (95% CI 0.42-1.21)).

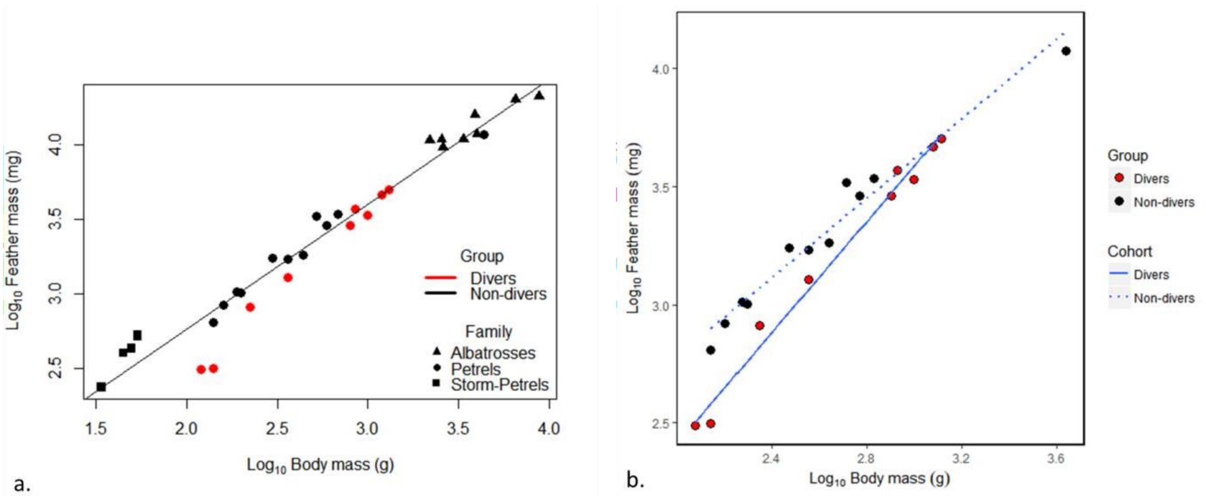


Figure 2.6. The influence of diving behaviour on the relationship between primary feather mass and body mass among (a) 33 species of Procellariiformes (slope: 0.84 (95% CI 0.77-0.91) and intercept: 1.08 (95% CI 0.89-1.27)) and (b) 20 species of Procellariidae (slope: 0.96 (95% CI 0.82-1.11) and intercept: 0.71 (95% CI 0.32-1.10)).

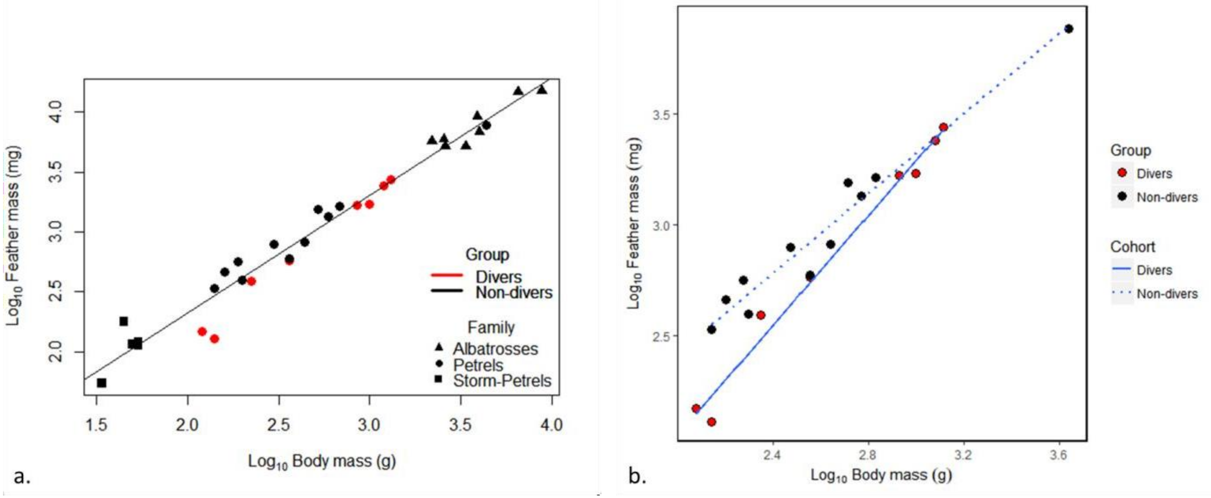


Figure 2.7. The influence of diving behaviour on the relationship between secondary feather mass and body mass among (a) 32 species of Procellariiformes (slope: 0.98 (95% CI 0.92-1.05) and intercept: 0.35 (95% CI 0.18-0.54)) and (b) 19 species of Procellariidae (slope: 1.03 (95% CI 0.87-1.19) and intercept: 0.22 (95% CI -0.20-0.65)).

Again, with the individual primaries the diving birds were found to be positively allometric from P4-P10, while the non-diving birds were found to be negatively allometric across all primaries (Table 2.7). The family level showed isometry from P5-P10, while the order level showed negative allometry throughout. There were no significant differences in primary feather masses relative to body mass between birds that use their wings for underwater propulsion and those that do not (Appendix 2). Secondaries of diving birds showed a tendency towards negative allometry throughout, but the 95% CIs included isometry. Birds that do not use their wings for underwater propulsion, family and order groups showed negative allometry throughout (Table 2.8).

Table 2.7: The allometric relationships between primary feather masses and body mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.77 (0.66-0.87)	-0.14 (-0.41-0.13)	0.96***
	Divers	0.92 (0.86-0.99)	-0.64 (-0.82- -0.46)	0.99***
	Procellariidae	0.82 (0.73-0.91)	-0.74 (-1.28- -0.20)	0.95***
	Procellariiformes	0.78 (0.72-0.83)	-0.17 (-0.32- -0.02)	0.96***
P2	Non-divers	0.80 (0.69-0.91)	-0.15 (-0.4-0.13)	0.97***
	Divers	0.93 (0.85-1.01)	-0.60 (-0.80- -0.39)	0.99***
	Procellariidae	0.84 (0.75-0.93)	-0.30 (-0.55- -0.05)	0.95***
	Procellariiformes	0.77 (0.72-0.82)	-0.08 (-0.23-0.07)	0.96***
P3	Non-divers	0.80 (0.68-0.91)	-0.02 (-0.34-0.29)	0.96***
	Divers	0.99 (0.88-1.10)	-0.66 (-0.96- -0.35)	0.98***
	Procellariidae	0.86 (0.75-0.98)	-0.24 (-0.56- -0.06)	0.93***

	Procellariiformes	0.77 (0.71-0.82)	0.07 (-0.29-0.43)	0.96***
P4	Non-divers	0.82 (0.68-0.95)	0.04 (-0.31-0.38)	0.95***
	Divers	1.06 (0.94-1.19)	-0.77 (-1.10- -0.43)	0.98***
	Procellariidae	0.90 (0.77-1.04)	-0.25 (-0.62-0.11)	0.91***
	Procellariiformes	0.78 (0.72-0.85)	0.10 (-0.08-0.27)	0.95***
P5	Non-divers	0.83 (0.69-0.97)	0.10 (-0.27-0.47)	0.95***
	Divers	1.15 (1.06-1.24)	-0.91 (-1.15- -0.66)	0.99***
	Procellariidae	0.95 (0.80-1.09)	-0.27 (-0.66-0.11)	0.91***
	Procellariiformes	0.81 (0.74-0.88)	0.13 (-0.06-0.32)	0.95***
P6	Non-divers	0.85 (0.71-0.99)	0.12 (-0.24-0.49)	0.95***
	Divers	1.20 (1.10-1.30)	-0.96 (-1.23- -0.69)	0.99***
	Procellariidae	0.98 (0.83-1.13)	-0.28 (-0.69-0.12)	0.90***
	Procellariiformes	0.83 (0.76-0.91)	0.14 (-0.06-0.35)	0.94***
P7	Non-divers	0.85 (0.70-1.00)	0.19 (-0.21-0.57)	0.94***
	Divers	1.24 (1.12-1.35)	-1.01 (-1.31- -0.70)	0.98***
	Procellariidae	0.99 (0.83-1.16)	-0.27 (-0.70-0.16)	0.90***
	Procellariiformes	0.85 (0.77-0.93)	0.17 (-0.05-0.39)	0.94***
P8	Non-divers	0.86 (0.72-0.99)	0.21 (-0.15-0.56)	0.95***
	Divers	1.26 (1.13-1.38)	-1.02 (-1.36- -0.69)	0.99***
	Procellariidae	1.00 (0.84-1.17)	-0.26 (-0.70-0.19)	0.90***
	Procellariiformes	0.86 (0.78-0.94)	0.19 (-0.03-0.41)	0.94***
P9	Non-divers	0.86 (0.74-0.99)	0.22 (-0.10-0.54)	0.96***
	Divers	1.27 (1.12-1.41)	-1.01 (-1.40- -0.62)	0.98***
	Procellariidae	1.01 (0.85-1.18)	-0.25 (-0.68-0.19)	0.90***
	Procellariiformes	0.86 (0.79-0.95)	0.20 (-0.02-0.42)	0.94***
P10	Non-divers	0.90 (0.80-0.99)	0.14 (-0.11-0.40)	0.98***
	Divers	1.20 (1.06-1.34)	-0.81 (-1.19- -0.42)	0.98***
	Procellariidae	1.01 (0.88-1.14)	-0.21 (-0.57-0.14)	0.93***
	Procellariiformes	0.89 (0.82-0.95)	0.15 (-0.04-0.33)	0.96***

*P<0.05 **P<0.01 ***P<0.001

Table 2.8: The allometric relationships between secondary feather masses and body mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.80 (0.69-0.91)	-0.25 (-0.53-0.03)	0.97***
	Divers	0.99 (0.84-1.14)	-0.88 (-1.30- -0.47)	0.97***
	Procellariidae	0.87 (0.75-0.99)	-0.48 (-0.80- -0.16)	0.93***
	Procellariiformes	0.76 (0.71-0.82)	-0.19 (-0.35- -0.02)	0.96***
S2	Non-divers	0.79 (0.67-0.91)	-0.29 (-0.60-0.02)	0.96***
	Divers	0.99 (0.84-1.14)	-0.93 (-1.33- -0.53)	0.97***
	Procellariidae	0.86 (0.74-0.98)	-0.53 (-0.85- -0.21)	0.93***
	Procellariiformes	0.77 (0.71-0.83)	-0.25 (-0.42- -0.08)	0.96***
S3	Non-divers	0.77 (0.64-0.90)	-0.28 (-0.61-0.06)	0.95***
	Divers	0.97 (0.83-1.12)	-0.95 (-1.32- -0.57)	0.98***
	Procellariidae	0.84 (0.72-0.97)	-0.53 (-0.86- -0.19)	0.92***
	Procellariiformes	0.75 (0.69-0.82)	-0.25 (-0.43- -0.08)	0.95***
S4	Non-divers	0.75 (0.61-0.89)	-0.26 (-0.62-0.10)	0.94***
	Divers	0.96 (0.84-1.09)	-0.93 (-1.27- -0.60)	0.98***
	Procellariidae	0.83 (0.71-0.95)	-0.52 (-0.84- -0.19)	0.92***
	Procellariiformes	0.75 (0.69-0.81)	-0.28 (-0.45- -0.11)	0.95***
S5	Non-divers	0.74 (0.60-0.88)	-0.26 (-0.63-0.11)	0.93***
	Divers	0.95 (0.81-1.09)	-0.92 (-1.29- -0.56)	0.98***
	Procellariidae	0.82 (0.70-0.94)	-0.51 (-0.83- -0.19)	0.92***
	Procellariiformes	0.75 (0.69-0.81)	-0.28 (-0.45- -0.12)	0.95***
S6	Non-divers	0.74 (0.60-0.88)	-0.27 (-0.65-0.10)	0.93***
	Divers	0.93 (0.79-1.07)	-0.87 (-1.24- -0.51)	0.98***
	Procellariidae	0.81 (0.69-0.93)	-0.50 (-0.81- -0.19)	0.92***
	Procellariiformes	0.75 (0.69-0.81)	-0.31 (-0.48- -0.15)	0.96***
S7	Non-divers	0.74 (0.60-0.87)	-0.28 (-0.63-0.08)	0.94***
	Divers	0.93 (0.79-1.06)	-0.87 (-1.22- -0.51)	0.98***
	Procellariidae	0.81 (0.69-0.92)	-0.50 (-0.80- -0.20)	0.93***
	Procellariiformes	0.75 (0.70-0.81)	-0.34 (-0.51- -0.17)	0.96***
S8	Non-divers	0.73 (0.59-0.86)	-0.24 (-0.59-0.11)	0.94***
	Divers	0.93 (0.79-11.06)	-0.88 (-1.25- -0.51)	0.98***
	Procellariidae	0.80 (0.68-0.92)	-0.48 (-0.80- -0.17)	0.92***
	Procellariiformes	0.76 (0.71-0.82)	-0.37 (-0.54- -21)	0.96***
S9	Non-divers	0.69 (0.47-0.91)	-0.18 (-0.76-0.39)	0.83***
	Divers	0.94 (0.79-1.10)	-0.93 (-1.35- -0.52)	0.97***
	Procellariidae	0.79 (0.64-0.94)	-0.48 (-0.87- -0.08)	0.87***
	Procellariiformes	0.76 (0.70-0.83)	-0.40 (-0.59- -0.20)	0.94***
S10	Non-divers	0.71 (0.57-0.86)	-0.22 (-0.59-0.16)	0.93***
	Divers	0.97 (0.80-1.15)	-1.02 (-1.50- -0.54)	0.96***
	Procellariidae	0.81 (0.67-0.95)	-0.52 (-0.89- -0.16)	0.89***
	Procellariiformes	0.81 (0.74-0.74)	-0.54 (-0.75 – 0.33)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Feather mass relative to feather length

As expected, there was a strong correlation between feather length and feather mass. Primaries and all flight feathers showed significant differences between the birds that use their wings to pursue prey underwater and those that only use their wings for propulsion in air and shallow depths. The primaries of non-divers and all Procellariiformes (Table 2.9) were positively allometric, whereas divers and Procellariidae were negatively allometric. However, the observed results from all flight feathers (Figure 2.8), primaries (Figure 2.9) and secondaries (Figure 2.10) show that diving birds invested slightly more mass in their flight feathers relative to feather length than non- diving petrels.

Table 2.9: The allometric relationships between total feather length and feather mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Total	Non-divers	2.40 (2.32-2.48)	-5.02 (-5.33- -4.72)	0.99***
	Divers	2.24 (2.13-2.34)	-4.34 (-4.76- -4.01)	1.00***
	Procellariidae	2.30 (2.13-2.46)	-4.64 (-5.22- -4.05)	0.98***
	Procellariiformes	2.35 (2.27-2.43)	-4.83 (-5.11- -4.55)	0.90***
Primaries	Non-divers	3.27 (3.16-3.37)	-7.22 (-7.56- -6.89)	0.99***
	Divers	2.73 (2.60-2.87)	-5.41 (-5.84- -4.99)	1.00***
	Procellariidae	2.76 (2.57-2.96)	-5.56 (-6.18- -4.93)	0.98***
	Procellariiformes	3.08 (2.93-3.22)	-6.59 (-7.06- -6.12)	0.98***
Secondaries	Non-divers	2.06 (1.99-2.14)	-3.71 (-3.97- -3.46)	0.99***
	Divers	1.94 (1.82-2.05)	-3.27 (-3.64- -2.90)	1.00***
	Procellariidae	2.03 (1.88-2.18)	-3.61 (-4.10- -3.12)	0.98***
	Procellariiformes	2.03 (1.97-2.10)	-3.61 (-3.83- -3.40)	0.99***

*P<0.05 **P<0.01 ***P<0.001

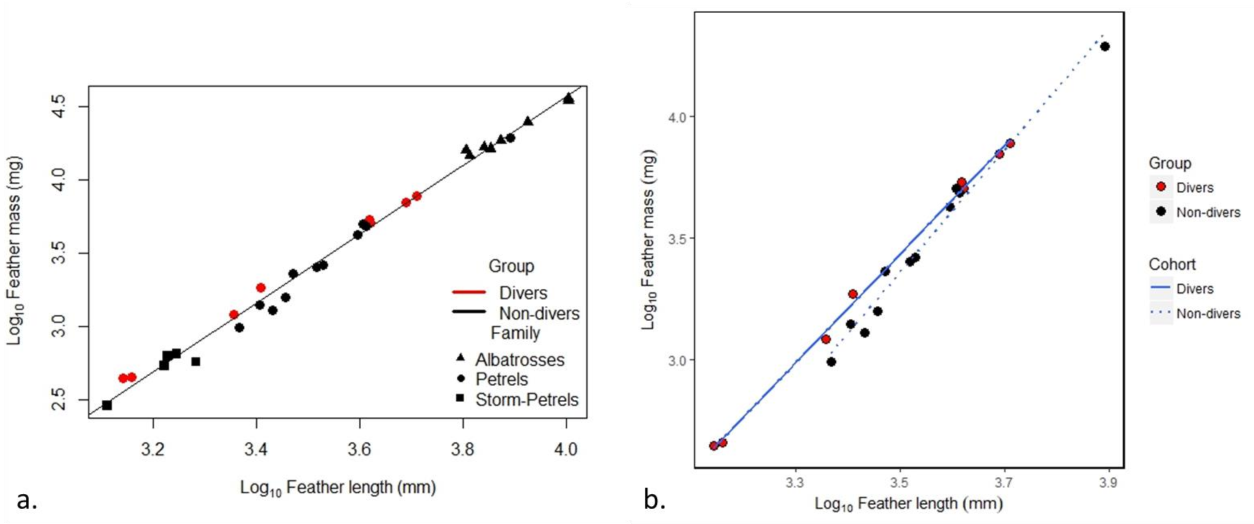


Figure 2.8. The influence of diving behaviour on the relationship between flight feather mass and feather length among (a) 33 species of Procellariiformes (slope: 2.35 (95% CI 2.27-2.43) and intercept: -4.83 (95% CI -5.11-0-4.55)) and (b) 20 species of Procellariidae (slope: 2.30 (95% CI 2.13-2.46) and intercept: -4.64 (95% CI -5.22- -4.05)).

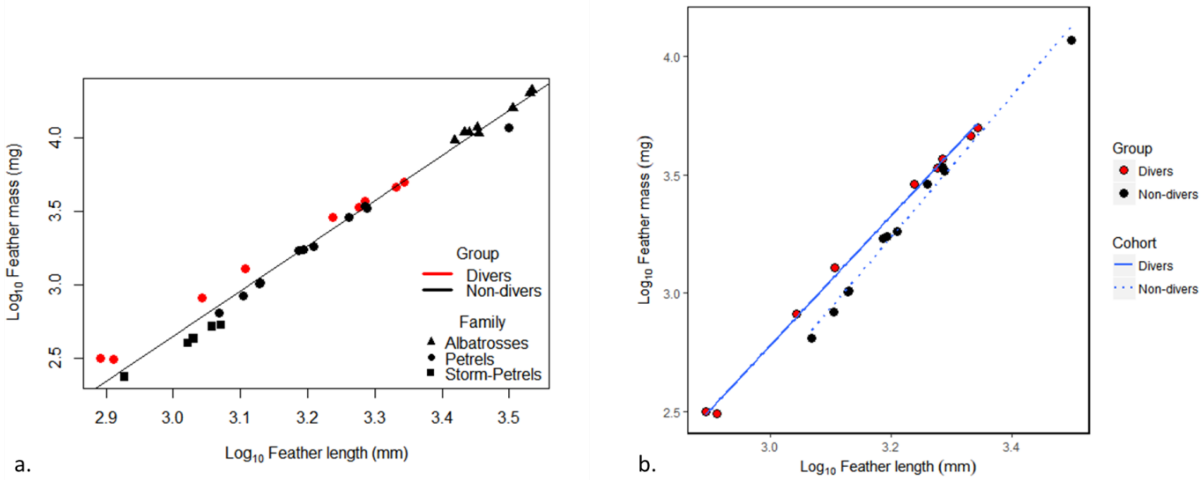


Figure 2.9. The influence of diving behaviour on the relationship between primary feather mass and feather length among (a) 33 species of Procellariiformes (slope: 3.08 (95% CI 2.93-3.22) and intercept: -6.59 (95% CI -7.06- -6.12)) and (b) 20 species of Procellariidae (slope: 2.30 (95% CI 2.13-2.46) and intercept: -5.56 (95% CI -6.18- -4.93)).

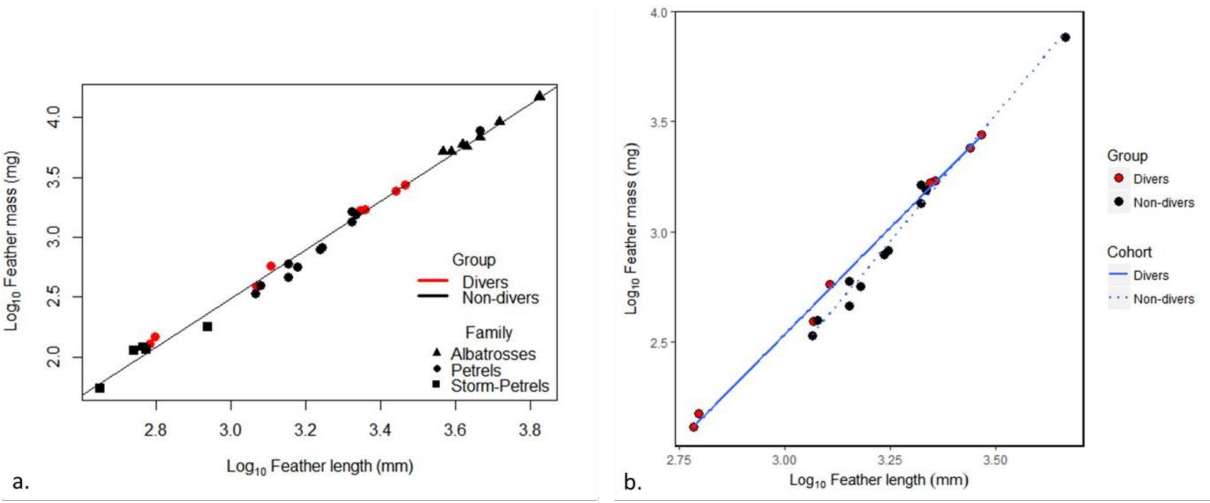


Figure 2.10. The influence of diving behaviour on the relationship between secondary feather mass and feather length among (a) 33 species of Procellariiformes (slope: 2.03 (95% CI 1.97-2.10) and intercept: -3.61 (95% CI -3.83- -3.40)) and (b) 20 species of Procellariidae (slope: 2.03 (95% CI 1.88-2.18) and intercept: -3.61 (95% CI -4.10- -3.12)).

Once again, the differences were most marked in the outer primaries, with P7-10 showing significant differences between divers and non-divers, whereas the inner primaries showed no significant differences (Table 2.10). Only the order level showed positive allometry, while the other three groups showed negative allometry, but the 95% CIs of non-diving birds included positive allometry.

Table 2.10: The allometric relationships between individual primary feather length and feather mass among various groups of procellariform seabirds.

Feather	**Group**	**Slope (95% CI)**	**Intercept (95% CI)**	**R^2**
P1	Non-divers	2.63 (2.17-3.09)	-3.45 (-4.38- -2.51)	0.94***
	Divers	2.76 (2.56-2.97)	-3.63 (-4.04- -3.23)	0.99***
	Procellariidae	2.65 (2.37-2.93)	-3.46 (-4.01- -2.90)	0.96***
	Procellariiformes	3.09 (2.91-3.27)	-4.35 (-4.72- -3.99)	0.97***
P2	Non-divers	2.69 (2.36-3.10)	-3.69 (-4.45- -2.93)	0.97***
	Divers	2.73 (2.51-2.95)	-3.62 (-4.06- -3.18)	0.99***
	Procellariidae	2.70 (2.48-2.92)	-3.59 (-4.05- -3.13)	0.97***
	Procellariiformes	3.10 (2.94-3.27)	-4.43 (-4.79- -4.08)	0.97***
P3	Non-divers	2.69 (2.32-3.05)	-3.64 (-4.41- -2.87)	0.97***
	Divers	2.69 (2.50-2.88)	-3.58 (-3.97- -3.18)	0.99***
	Procellariidae	2.64 (2.42-2.86)	-3.51 (-3.98- -3.04)	0.97***
	Procellariiformes	3.06 (2.89-3.23)	-4.41 (-4.77- -4.05)	0.98***
P4	Non-divers	2.80 (2.48-3.11)	-3.92 (-4.61- -3.23)	0.98***
	Divers	2.67 (2.48-2.87)	-3.58 (-3.99- -3.16)	0.99***
	Procellariidae	2.67 (2.46-2.88)	-3.61 (-4.06- -3.17)	0.97***
	Procellariiformes	3.06 (2.90-3.21)	-4.45 (-4.79- -4.10)	0.98***
P5	Non-divers	2.85 (2.59-3.11)	-4.06 (-5.65- -3.48)	0.98***

	Divers	2.70 (2.58-2.82)	-3.65 (-3.90- -3.39)	1.00***
	Procellariidae	2.70 (2.50-2.89)	-3.69 (-4.11- -3.26)	0.98***
	Procellariiformes	3.05 (2.89-3.20)	-4.47 (-4.82- -4.12)	0.98***
P6	Non-divers	3.05 (2.93-3.17)	-4.54 (-4.81- -4.27)	1.00***
	Divers	2.66 (2.53-2.80)	-3.59 (-3.89- -3.28)	1.00***
	Procellariidae	2.73 (2.53-2.92)	-3.78 (-4.22- -3.34)	0.98***
	Procellariiformes	3.06 (2.91-3.21)	-4.54 (-4.88- -4.19)	0.98***
P7	Non-divers	3.18 (3.07-3.29)	-4.86 (-5.11- -4.61)	1.00***
	Divers	2.63 (2.35-2.90)	-3.51 (-4.11- -2.90)	0.98***
	Procellariidae	2.72 (2.48-2.97)	-3.77 (-4.33- -3.22)	0.97***
	Procellariiformes	3.02 (2.85-3.19)	-4.47 (-4.86- -4.08)	0.98***
P8	Non-divers	3.01 (2.83-3.20)	-4.51 (-4.94- -4.08)	1.00***
	Divers	2.67 (2.52-2.83)	-3.64 (-3.99- -3.29)	1.00***
	Procellariidae	2.71 (2.51-2.92)	-3.78 (-4.24- -3.32)	0.98***
	Procellariiformes	3.03 (2.87-3.18)	-4.52 (-4.88 – 4.15)	0.98***
P9	Non-divers	3.09 (2.95-3.22)	-4.67 (-4.99- -4.35)	1.00***
	Divers	2.66 (2.54-2.78)	-3.60 (-3.86- -3.34)	1.00***
	Procellariidae	2.73 (2.53-2.93)	-3.81 (-4.25- -3.37)	0.98***
	Procellariiformes	3.02 (2.87-3.16)	-4.48 (-4.82- -4.15)	0.98***
P10	Non-divers	3.04 (2.90-3.18)	-4.52 (-4.85- -4.19)	1.00***
	Divers	2.46 (2.32-2.61)	-3.10 (-3.42- -2.78)	1.00***
	Procellariidae	2.59 (2.36-2.81)	-3.43 (-3.95- -2.91)	0.97***
	Procellariiformes	2.89 (2.74-3.04)	-4.14 (-4.48- -3.80)	0.98***

*P<0.05 **P<0.01 ***P<0.001

The individual secondary feathers of non-diving birds and Procellariiformes showed positive allometry while the divers and Procellariidae showed negative allometry, but some feathers of Procellariidae showed 95% CIs including positive allometry (Table 2.11). Secondaries S1-S5 and S9 showed no significant differences while S6-S8 and S10 showed significant differences between petrels that dive underwater and those that do not.

Table 2.11: The allometric relationships between individual secondary feather length and feather mass among various groups of procellariform seabirds.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	3.03 (2.62-3.43)	-4.17 (-4.97- -3.37)	0.97***
	Divers	2.72 (2.54-2.89)	-3.50 (-3.84- -3.17)	1.00***
	Procellariidae	2.80 (2.58-3.03)	-3.71 (-4.16- -3.26)	0.97***
	Procellariiformes	3.00 (2.84-3.16)	-4.12 (-4.44- -3.80)	0.98***
S2	Non-divers	3.16 (2.67-3.65)	-4.46 (-5.43- -3.48)	0.95***
	Divers	2.75 (2.55-2.95)	-3.59 (-3.97- -3.21)	0.99***
	Procellariidae	2.86 (2.57-3.14)	-3.83 (-4.38- -3.28)	0.96***
	Procellariiformes	3.10 (2.92-3.28)	-4.34 (-4.70- -3.99)	0.98***
S3	Non-divers	3.22 (2.71-3.73)	-4.60 (-5.61- -3.59)	0.95***
	Divers	2.75 (2.55-2.96)	-3.62 (-4.01- -3.23)	0.99***
	Procellariidae	2.86 (2.57-3.16)	-3.87 (-4.45- -3.30)	0.96***
	Procellariiformes	3.11 (2.93-3.28)	-4.37 (-4.71- -4.02)	0.98***
S4	Non-divers	3.25 (2.78-3.72)	-4.69 (-5.60- -3.77)	0.96***
	Divers	2.74 (2.56-2.93)	-3.63 (-3.98- -3.28)	0.99***
	Procellariidae	2.87 (2.59-3.16)	-3.92 (-4.47- -3.37)	0.96***
	Procellariiformes	3.07 (2.93-3.22)	-4.32 (-4.61- -4.03)	0.98***
S5	Non-divers	3.21 (2.79-3.63)	-4.62 (-5.45- -3.79)	0.97***
	Divers	2.76 (2.67-2.85)	-3.68 (-3.85- -3.50)	1.00***
	Procellariidae	2.87 (2.61-3.13)	-3.94 (-4.44- -3.43)	0.97***
	Procellariiformes	3.02 (2.89-3.16)	-4.24 (-4.52- -3.97)	0.98***
S6	Non-divers	3.23 (2.86-3.60)	-4.68 (-5.40- -3.96)	0.98***
	Divers	2.64 (2.50-2.77)	-3.46 (-3.71- -3.20)	1.00***
	Procellariidae	2.80 (2.54-3.06)	-3.81 (-4.32- -3.30)	0.97***
	Procellariiformes	2.99 (2.85-3.13)	-4.20 (-4.47- -3.92)	0.98***
S7	Non-divers	3.24 (2.72-3.76)	-4.72 (-5.73- -3.71)	0.95***
	Divers	2.57 (2.42-2.71)	-3.34 (-3.61- -3.06)	1.00***
	Procellariidae	2.74 (2.43-3.06)	-3.71 (-4.32- -3.10)	0.95***
	Procellariiformes	2.95 (2.80-3.09)	-4.12 (-4.40- -3.83)	0.98***
S8	Non-divers	3.22 (2.78-3.65)	-4.66 (-5.51- -3.81)	0.97***
	Divers	2.48 (2.32-2.64)	-3.15 (-3.46- -2.84)	1.00***
	Procellariidae	2.67 (2.38-2.96)	-3.55 (-4.12- -2.99)	0.95***
	Procellariiformes	2.93 (2.78-3.08)	-4.08 (-4.38- -3.78)	0.98***
S9	Non-divers	3.12 (2.33-3.90)	-4.50 (-6.05-2.96)	0.89***
	Divers	2.43 (2.27-2.59)	-3.07 (-3.38- -2.77)	0.99***
	Procellariidae	2.57 (2.17-2.96)	-3.39 (-4.16- -2.61)	0.91***
	Procellariiformes	2.88 (2.70-3.06)	-4.01 (-4.37- -3.66)	0.97***
S10	Non-divers	3.19 (2.83-3.54)	-4.62 (-5.32- -3.92)	0.98***
	Divers	2.38 (2.23-2.53)	-2.97 (-3.26- -2.67)	1.00***
	Procellariidae	2.55 (2.27-2.83)	-3.33 (-3.88- -2.78)	0.95***
	Procellariiformes	2.85 (2.71-2.98)	-3.93 (-4.20- -3.66)	0.98***

*P<0.05 **P<0.01 ***P<0.001

Feather width and barb length relative to feather length

I used average values for each species to test allometry; each section was averaged separately (e.g. Sooty Shearwater had averages for base, middle and tip) and after accounting for differences in body size, there were no significant differences in either barb length or feather width between divers and non-divers. Moreover, there were no significant differences between groups when accounting for feather length, for either primaries or secondaries. Even when testing at three locations along the vane, no significant differences were found (Table 2.12; Appendix 3a-10b). However, the allometric relationship for secondaries of petrels that dive tended to have a steeper slope than non-diving species. When relating feather width to feather length, diving birds tended to have broader feathers (Appendix 3a-4b). This is most obvious for the outer primaries, where diving birds lie above the regression line while the non-diving birds lie below the regression (Appendix 4c). Again, this pattern was more evident in the diving petrels and *Puffinus* species. The tips of feathers are subjected to most of the forces distributed along the vane, so I expected any differences to be more marked at the tips, but again there were no significant differences between diving and non- diving birds. Both primaries (Appendix 7a) and secondaries (Appendix 7b) showed similar results, while the outer primaries (Appendix 8c) showed that diving birds have longer barbs compared to the non-diving birds because they lie above the regression line.

Table 2.12: The allometric relationships between barb length and feather length among 20 Procellariidae species.

Feather	Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Primaries	Tip	Non-divers	0.77 (0.59-0.94)	-0.17 (-0.73-0.39)	0.91**
		Divers	0.71 (0.60-0.81)	0.04 (-0.29-0.37)	0.97**
		Procellariidae	0.72 (0.63-0.81)	0.00 (-0.28-0.28)	0.94**
Secondaries		Non-divers	0.83 (0.75-0.90)	-0.04 (-0.29-0.22)	0.98**
		Divers	1.04 (0.85-1.23)	-0.74 (-1.34- -0.15)	0.96**
		Procellariidae	0.96 (0.87-1.07)	-0.53 (-0.85--2.21)	0.96**
Primaries	Middle	Non-divers	0.84 (0.73-0.96)	-0.25 (-0.63-0.12)	0.96**
		Divers	0.74 (0.64-0.83)	0.13 (-0.18-0.43)	0.98**
		Procellariidae	0.76 (0.68-0.84)	0.04 (-0.22-0.30)	0.95**
Secondaries		Non-divers	0.76 (0.58-0.94)	0.36 (-0.23-0.95)	0.90**
		Divers	1.03 (0.86-1.19)	-0.52 (-1.06-0.02)	0.97**
		Procellariidae	0.94 (0.82-1.06)	-0.25 (-0.63-0.14)	0.94**
Primaries	Base	Non-divers	0.91(0.83-0.99)	-0.41 (-0.67 --0.15)	0.99**
		Divers	0.84 (0.70-0.97)	-0.14 (-0.58-0.28)	0.96**
		Procellariidae	0.84 (0.75-0.93)	-1.18 (-0.46-0.11)	0.96**
Secondaries		Non-divers	0.78 (0.64-0.93)	0.24 (-0.24-0.70)	0.94**
		Divers	1 (0.82-1.18)	-0.45 (-1.03-0.12)	0.96**
		Procellariidae	0.92 (0.82-1.02)	-0.22 (-0.56-0.12)	0.95**

*P<0.05 **P<0.01 ***P<0.001

Table 2.13: The allometric relationships between vane width and feather length among 20 Procellariidae species.

Feather	Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Primaries	Tip	Non-divers	0.79 (0.65-0.92)	0.04 (-0.39-0.48)	0.95**
		Divers	0.72 (0.62-0.82)	0.29 (-0.33-0.61)	0.97**
		Procellariidae	0.73 (0.64-0.81)	0.25 (-0.01-0.51)	0.95**
Secondaries		Non-divers	1.11 (0.80-1.41)	0.05 (-0.36-0.46)	0.87**
		Divers	0.81 (0.42-1.13)	-0.30 (-0.67-0.06)	0.84**
		Procellariidae	0.94 (0.87-1.01)	-0.18 (-0.41-0.06)	0.98**
Primaries	Middle	Non-divers	0.80 (0.65-0.95)	0.16 (-0.36-0.59)	0.94**
		Divers	0.70 (0.60-0.81)	0.45 (0.11-0.79)	0.97**
		Procellariidae	0.72 (0.62-0.81)	0.40 (0.09-0.70)	0.93**
Secondaries		Non-divers	0.87 (0.74-0.99)	0.36 (-0.20-0.91)	0.96**
		Divers	0.98 (0.86-1.09)	-0.20 (-0.54-0.14)	0.98**
		Procellariidae	0.94 (0.85-1.03)	-0.01 (-0.30-0.28)	0.96**
Primaries	Base	Non-divers	0.84 (0.75-0.94)	0.01 (-0.30-0.32)	0.98**
		Divers	0.77 (0.65-0.89)	0.28 (-0.09-0.65)	0.97**
		Procellariidae	0.78 (0.69-0.86)	0.24 (-0.03-0.51)	0.95**
Secondaries		Non-divers	0.83 (0.66-1.00)	0.26 (-0.22-0.75)	0.92**
		Divers	1.00 (0.89-1.11)	-0.02 (-0.40-0.37)	0.99**
		Procellariidae	0.89 (0.81-0.98)	0.11 (-0.16-0.38)	0.97**

*P<0.05 **P<0.01 ***P<0.001

Barb and barbule density relative to feather length

I used average values for each species to test allometry; each section was averaged separately (e.g. Sooty Shearwater had averages for base, middle and tip). Barb density decreased slightly with increasing feather size (Table 2.14), and the rate of decrease tended to be greater among petrels that dive, but they did not differ significantly compared to the non-diving birds (Table 2.14). Barbule density was largely independent of feather size and further, no significant differences were found between the diving birds and the non-diving birds (Tables 2.15-2.16; Appendix 11-12).

Table 2.14: The allometric relationships between barb density and primary feather length among of 20 species of Procellariidae.

Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Non-divers	-0.12 (-0.23- -0.01)	2.68 (2.34-3.02)	0.43**
	Divers	-0.23 (-0.23- -0.03)	2.70 (2.38-3.01)	0.57*
	Procellariidae	-0.12 (-0.19- -0.04)	2.66 (2.43-2.89)	0.39*
Middle	Non-divers	-0.11 (-0.20- -0.01)	2.65 (2.34-2.95)	0.44*
	Divers	-0.18 (-0.23- -0.13)	2.85 (2.69-3.01)	0.91**
	Procellariidae	-0.14 (-0.21- -0.08)	2.75 (2.55-2.95)	0.59**
Base	Non-divers	-0.11 (-0.21-0.00)	2.70 (2.36-3.04)	0.38*
	Divers	-0.32 (-0.41- -0.23)	3.34 (3.05-3.62)	0.91**
	Procellariidae	-0.23 (-0.33- -0.13)	3.07 (2.76-3.38)	0.60**

*P<0.05 **P<0.01 ***P<0.001

Table 2.15: The allometric relationships between barbule density (in the middle of the vane) and primary feather length among 20 species of Procellariidae.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	-0.13 (-0.61-0.36)	1.55 (0.59-2.52)	-0.10
	Divers	-0.02 (-0.30-0.27)	1.34 (0.77-1.92)	-0.19
	Procellariidae	-0.03 (-0.21-0.14)	1.37 (1.02-1.73)	-0.07
P4	Non-divers	-0.07 (-0.42-0.29)	1.45 (0.69-2.20)	-0.15
	Divers	-0.07 (-0.27-0.14)	1.44 (1.01-1.87)	-0.05
	Procellariidae	-0.06 (-0.19-0.06)	1.44 (1.18-1.71)	0.02
P6	Non-divers	-0.05 (-0.38-0.28)	1.44 (0.71-2.16)	-0.16
	Divers	0.05 (-0.03-0.13)	1.21 (1.03-1.40)	0.20
	Procellariidae	0.03 (-0.05-0.12)	1.25 (1.06-1.43)	-0.01
P8	Non-divers	-0.03 (-0.45-0.40)	1.38 (0.43-2.33)	-0.19
	Divers	0.05 (-0.12-0.23)	1.22 (0.83-1.60)	-0.07
	Procellariidae	0.04 (-0.09-0.16)	1.24 (0.96-1.52)	-0.04
P10	Non-divers	0.11 (-0.27-0.49)	1.10 (0.26-1.94)	-0.08
	Divers	0.07 (-0.14-0.27)	1.21 (0.75-1.67)	-0.05
	Procellariidae	0.07 (-0.06-0.20)	1.20 (0.91-1.49)	0.03

*P<0.05 **P<0.01 ***P<0.001

Table 2.16: The allometric relationships between barbule density (at the feather tip) and primary feather length among 20 species of Procellariidae.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	0.02 (-0.56-0.59)	1.26 (0.11-2.41)	-0.20
	Divers	0.04 (-0.22-0.290	1.24 (0.72-1.75)	-0.17
	Procellariidae	0.04 (-0.14-0.22)	1.23 (0.87-1.59)	-0.07
P4	Non-divers	0.30 (-0.21-0.81)	0.67 (-0.40-1.75)	-0.18
	Divers	0.04 (-0.14-0.21)	1.24 (0.86-1.61)	-0.14
	Procellariidae	0.07 (-0.08-0.22)	1.16 (0.85-1.47)	0.01
P6	Non-divers	0.09 (-0.37-0.56)	1.10 (0.07-2.12)	-0.14
	Divers	-0.01 (-0.09-0.08)	1.32 (1.13-1.50)	-0.20
	Procellariidae	0.01 (-0.10-0.11)	1.29 (1.06-1.52)	-0.08
P8	Non-divers	0.07 (-0.43-0.57)	1.15 (0.02-2.29)	-0.17
	Divers	-0.04 (-0.13-0.06)	1.39 (1.18-1.60)	0.00
	Procellariidae	-0.02 (-0.13-0.09)	1.36 (1.11-1.61)	-0.07
P10	Non-divers	0.01 (-0.42-0.43)	1.30 (0.36-1.24)	-0.20
	Divers	-0.07 (-0.25-0.11)	1.46 (1.07-1.86)	0.01
	Procellariidae	-0.06 (-0.19-0.06)	1.44 (1.17-1.72)	0.02

*P<0.05 **P<0.01 ***P<0.001

DISCUSSION

Wing shape and size have evolved differently in bird species to suit their specific habitat exploitation and flight characteristics (Rayner 1988; Pennycuick 1987a). Both wing shape and wing area are determined by the size and (to a lesser extent) shape of individual flight feathers, especially the outer primaries. In this chapter I investigated how flight feathers influence the size of wings among procellariiform seabirds, and whether there are differences in the flight feathers of petrels that use their wings for underwater propulsion and those that do not. Petrels that use their wings for underwater propulsion have relatively short wings compared to related species that seldom dive (Pennycuick 1987b, Chapter 1), but not much is known about their feathers. All Procellariiformes have ten primaries, but the number of secondaries varies with body size (Figure 2.1), so I also investigated the allometric relationship between the number of secondaries and wingspan.

Diving birds have evolved shorter flight feathers than non-diving species, presumably to reduce wing area, which is advantageous for underwater flight (Pennycuick 1987b). Long feathers induce drag stress when diving in pursuit of their prey (Wilson *et al*. 1992). Pennycuick (1987b) suggested that the short wings in wing-propelled birds is a result of selection pressures for using two physically different media. The conflicts between air and water have resulted in diving birds having to evolve the smallest wing area that still allows flight in air (Elliot *et al*. 2013). The differences in wing size associated with diving behaviour were more marked in the small petrels (especially diving-petrels) than the large *Procellaria* petrels. This may not necessarily imply that because they have short wings they can dive deeper. However, their small bodies allow flexibility in wing size, thus, dive efficiently and reach great depths underwater.

As expected, the differences between the divers and non-divers were more pronounced in the primaries than the secondaries, suggesting that selection for reduced wing area among diving species has focused more on wing length than wing breadth. This is so because the secondary feathers are not distinctively varied in terms of size, similar to feathers of birds that have rounded wings (Dawson 2005). Moreover, secondaries do not experience as much of the flight forces as the primaries because of their location on the inner wing and additional support from the secondary coverts. Within the primaries, I expected differences to be greater on the outer than the inner primaries, and indeed the outer primaries were shorter relative to body size in diving birds than non-diving birds. The outer primary feathers experience the greatest forces during flight; birds are therefore required to invest more on them to perform their suitable flight modes to the maximum.

Contrary to expectations, the feathers of diving birds weigh less relative to body mass than those of non-divers, but this is due to the shorter length of their feathers. When scaling feather mass with feather length, wing-propelled divers have slightly heavier flight feathers than non-divers – a trend also found by Dawson (2005). Again, differences were more marked in the primaries than the secondaries. Reduced feather length is necessary for flying in the much denser medium and the heaviness relative to the length presumably grants greater strength to withstand the force of operating in a much denser medium (but see Chapter 3).

Although there were no significant differences in feather width and barb density between divers and non-divers. The feather mass relative to feather length is probably supported by the minimal differences found feather widths and barbs (Appendix 3a-10b), the regression line showed that the divers had long feathers widths and barbs. The greater mass per unit length of diving petrels flight feathers (mainly the outer primaries) results from slightly wider feathers than expected for their length. This could simply be a consequence of selection for reduced feather length independent of feather width, or it could be to increase the overlap between adjacent feathers, thus strengthening the wing for use underwater. In all cases, the differences between diving and non-diving species were greater among small petrels. Smaller birds, such as the diving-petrels have a mechanical advantage and are better able to compromise the flight-diving trade-offs than bigger birds. The smaller diving birds can manage to fly in air with smaller wings relative to their mass. Thus deviate more from species evolved only for aerial flight (i.e. they have greater flexibility of wing form simply because they are small; just as there are limits to the upper size for powered flight in air because of the allometry of wing area to weight, so there are limits to the upper size for wings to work in both air and water (Pennycuick 1987b; Morris and Askew 2010). This presumably explains why there are no very effective wing-propelled divers weighing more than about 1 kg (with the exception of Penguins. As birds get bigger, their wings have to get larger faster than their body mass (because mass increases as the cube of body length, whereas wing area only increases as the square of length) and their flap rate decreases. Small birds can manage flight in air and water inherently better than larger birds, and by the time a bird gets to about 2 kg, it probably cannot manage to have wings suitable to fly effectively in both water an air (Figure 1.4).

Barb and barbule densities decreased with feather length. The diving-petrels had the shortest feathers and the greatest densities of barbs; this however, may be because smaller feathers may have denser barbs simply because they are small. There is a scaling relationship between elements of a feather and feather size, large feathers have thicker shafts, which mean they have larger barbs, and therefore, they have less dense feathers simply because they are large (Pap *et al.* 2015; 2016). So, because of this, conclusions on whether the diving birds have denser feathers compared to the non-diving birds relative to the feather length cannot be drawn. Moreover, diving-petrels have smaller bodies as a result they adopted flapping as their flight style, and the latter requires flight feathers to be denser, because they experience greater forces upon their wings than gliding or soaring species.

CONCLUSIONS

Even though diving-petrels are heavier than storm petrels, storm petrels have longer and heavier flight feathers, which confirm that the evolution of short wings derived from short feathers was aimed at an ability to use wings to ‘fly’ underwater. Feathersof diving birds were lighter relative to their body size (mass) compared with non- diving birds, but this is a consequence of their short feather length. Relative to feather size, diving birds have slightly heavier feathers, which are consistent with their use for propulsion in a much denser medium. However, this effect was minor and might be largely a consequence of selection for reduced length, because flight feathers of diving birds mainly differ in length and not width compared to non-diving petrels. It seems that wing-propelled diving birds have made relatively few structural adaptations to their flight feathers, and the main response to flapping in the much denser medium of water is to partly close the wing, further reducing wing area and increasing the strength of the wing through greater overlap between individual feathers.

CHAPTER 3: IS STIFFNESS OF PRIMARY FEATHERS INFLUENCED BY DIVING BEHAVIOUR AMONG PROCELLARIIFORMES?

Abstract

Flexural stiffness of flight feathers is expected to be greater for birds that use their wings for propulsion underwater as well as for flight because water is much denser than air. I tested whether primary feathers of diving birds have deeper rachises compared to non-diving birds (because previous studies have found that stiffness correlates with rachis depth) and compared the force required to bend flight feathers through a fixed angle between petrels that regularly dive >10 m and those that seldom use their wings to dive underwater. Flight feathers were inserted on a clamp and an arm applied pressure to the feather both dorsally and ventrally at three locations along the vane (one-quarter, half and three-quarters of the way from the base of the vane to the tip). Standardised major axis regressions (model II) were used to analyse the scaling relationships between rachis depth and feather stiffness relative to feather length and body mass. Diving behaviour had no clear effect on rachis depth, although the data were very noisy. Feather stiffness was similar among all birds, with no significant differences in allometry between diving and non-diving birds. When relating feather stiffness to body mass, feathers of diving birds were less stiff than those of non-diving birds as a consequence of their shorter flight feathers. However, diving birds exhibited slightly less flexure relative to the length of their flight feathers than non-diving birds, suggesting that their feathers are slightly stiffer. Overall, diving birds show little structural adaptation to their individual flight feathers, suggesting that most of the mechanical response to the much greater density of water comes from partly folding the wing when flapping underwater.

INTRODUCTION

Wings of birds are designed to withstand aerodynamic forces, which vary with flight mode, speed and flight duration (Pennycuick 1989). Hence, life-history and flight behaviour determine in part the investment in the structure of flight feathers (Worcester 1996; Aparicio *et al*. 2003; Weber *et al*. 2005; Lingham-Soliar *et al*. 2010; Bachmann *et al*. 2012; Wang *et al*. 2012). Flight feathers face most of the aerodynamic forces and thus need to be strong enough to avoid breakage during flight. Therefore, flexural stiffness of each feather (mainly determined by its rachis) determines how feathers are deflected during flight (Wang *et al*. 2012).

Wing or flight feathers can be subjected to large aerodynamic forces during flight, particularly the outer flight feathers (Worcester 1996, Chapter 2). Each flight feather consists of a vane (see Chapter 1), which is the part subjected to most of the forces, particularly on the outer parts of the feather than the inner end (which is protected by adjacent flight feathers and the coverts). The rachis reacts to the forces by bending, but just how much force can feathers withstand? Do these forces remain the same on different parts of a feather? Do the forces change depending on whether the wing is descending (downstroke) or ascending (upstroke)? Resistance to breakage during flight is determined by feather flexibility. Material and geometric properties determine how much a structure can bend, which is called flexural stiffness (Worcester 1996).

Flexural stiffness and other morphological features depend on size (see Chapters 1 and 2); so, to understand the general principles controlling mechanical properties of organisms, scaling analyses must be performed (Thompson 1961). Worcester (1996) scaled feather stiffness relative to body mass to determine whether flexural stiffness is dependent on body size, and compared the slopes of the scaling relationships. He tested two theories: geometric similarity (isometry) predicts that feathers sustain a constant (stationary) shape regardless of size, and elastic similarity predicts that feathers should experience similar elastic deformations under load regardless of size. His results obtained showed negative allometry in flexural stiffness, with larger birds having relatively more flexible feathers. Wang *et al*. (2012) argued that the equation used to calculate flexural stiffness by Worcester (1996) was inappropriate and that his sample size was too small to support his conclusions, but their larger sample size found similar results to Worcester (1996).

This chapter investigates the flexural stiffness of flight feathers from procellariiform birds. As described in Chapters 1 and 2, the petrels offer an ideal opportunity to test the structural implications of using wings for propulsion underwater as well as for aerial flight. Because water is much denser than air, diving birds need feathers that can utilise both media without damaging their feathers. So, I expect the rachis of the wing-propelled divers to be deep and robust, and their feathers more resistant to bending forces compared to closely-related birds that do not use their wings underwater. To confirm my expectations in this chapter I compare the diving and non-diving birds by testing 1) How rachis depth scales with flight feather length, 2) How stiffness scales with feather length, 3) How stiffness scale with body mass, and 4) How stiffness varies relative to different parts of the flight feather (base, middle and tip). Moreover, the body masses of the species vary considerably, the results were scaled relative to body size.

METHODS

Flight feathers (primaries) from birds in the order Procellariiformes were examined for rachis depth and feather stiffness. The forces experienced during flight are mainly borne by the rachis, therefore I measured the depth of the rachis across the dorsoventral section (Pap *et al*. 2015) with Vernier callipers to the nearest 0.02 mm at three locations along each feather vane: base, middle and tip (=75% from the base to the tip; Figure 1.1).

Feather stiffness was measured on alternate primary feathers (P2, P4, P6, P8 and P10) at the same three locations. Each feather was attached *via* its calamus (Figure 1.1) in a clamp that firmly held the feather without overly compressing its shape. The amount of feather held in the clamp was the same as that in the feather sheath on the bird. The entire clamp structure was on a slider mechanism (Figure 3.1) that allowed the test angle to be adjusted so that the force was applied at right angles to the vane. Tests were run on an Instron 3365 tension testing machine with a 100N load cell at 4mm/min. The three locations on each feather were tested on both the dorsal (equivalent to the upstroke resistance) and ventral (downstroke) sides of the vane. The programme Bluehill (2.15) was used to record the force throughout each test (Figure 3.2). The tests measured the force (N) required to bend each point through a series of angles (4º, 8º and 12º).

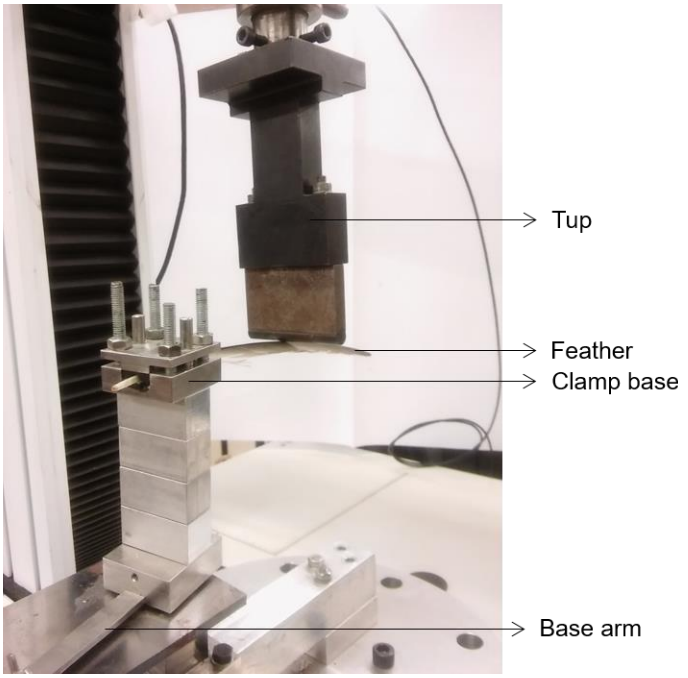


Figure 3.1. The Instron 3365 testing machine used to test stiffness of the feathers. In this case the resistance of P10 from a White-chinned Petrel is being tested to a force from above the feather, similar to the forces experienced during the upstroke.

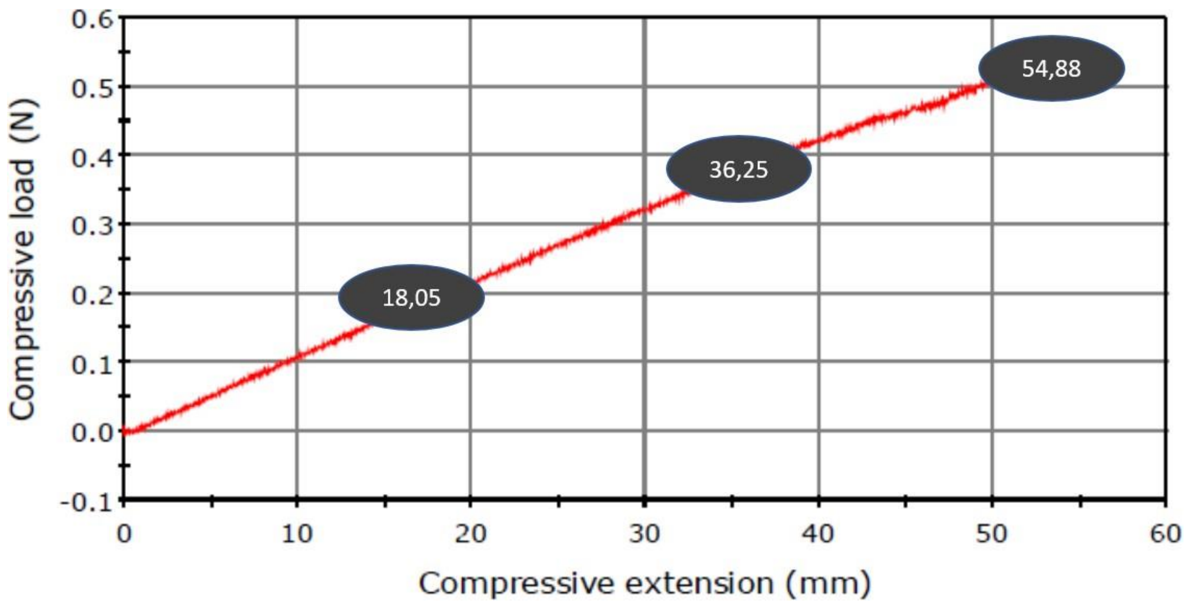


Figure 3.2. Force-displacement curve of the tip of primary 10 of a Wandering Albatross *Diomedea exulans*; the points illustrated are for the three different angles: 4, 8 and 12º.

Statistical analysis

I used model II regressions in R to scale rachis depth and feather stiffness with body mass and feather length (see Chapter 2 for details). Each section (base, middle and tip were analysed separately. I also examined how the force required to bend a feather through a fixed angle changed along the length of the feather, by expressing the force required to bend the middle and tip as a percentage of the force at the base.

RESULTS

Rachis depth relative to feather length

I expected rachis and calamus depth of birds that tend to dive >10 m underwater to be deeper than the birds that seldom use their wings for underwater propulsion, but there were no significant differences between the two groups, for either primaries or secondaries. Moreover, no significant differences were found along the vane, but the data were noisy, with no consistent pattern in allometric slopes (Appendices 13-17b).

Feather stiffness relative to feather length

I expected the flight feathers of the diving birds to be stiffer than those of the non- diving birds. However, the allometric relationships between the force required to bend through a fixed angle and feather length were not significantly different between diving and non-diving birds on either the upstroke (Table 3.1) or downstroke (Table 3.2). Location along the vane also had no significant effect for an 8º bend for all primaries (Tables 3.3 – 3.6, Figures 3.3 and 3.4), and similar results were observed when bending through 4º and 12º.

Table 3.1: The allometric relationships between feather length and stiffness (force required to bend the feathers through an 8º arc from above = upstroke) among various groups of procellariform seabirds.

Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Non-divers	2.11 (1.66-2.55)	-6.60 (-7.91- -5.30)	0.92***
	Divers	1.74 (1.39-2.10)	-5.53 (-6.54- -4.52)	0.94***
	Procellariidae	1.87 (1.62-2.11)	-5.89 (-6.61- -5.18)	0.93***
	Procellariiformes	2.21 (1.99-2.43)	-6.90 (-7.55- -6.25)	0.94***
Middle	Non-divers	1.93 (1.50-2.35)	-5.56 (-6.81- -4.31)	0.91***
	Divers	1.46 (0.95-1.96)	-4.22 (-5.67- -2.77)	0.85***
	Procellariidae	1.64 (1.34-1.94)	-4.74 (-5.61- -3.88)	0.88***
	Procellariiformes	2.10 (1.85-2.36)	-6.06 (-6.82- -5.29)	0.91***
Base	Non-divers	1.54 (0.82-2.26)	-3.92 (-6.03- -1.80)	0.69**
	Divers	1.04 (0.33-1.74)	-2.50 (-4.53- -0.48)	0.58*
	Procellariidae	1.25 (0.81-1.69)	-3.09 (-4.36- -1.82)	0.65**
	Procellariiformes	1.90 (1.53-2.27)	-4.93 (-6.01- -3.84)	0.81***

*P<0.05 **P<0.01 ***P<0.001

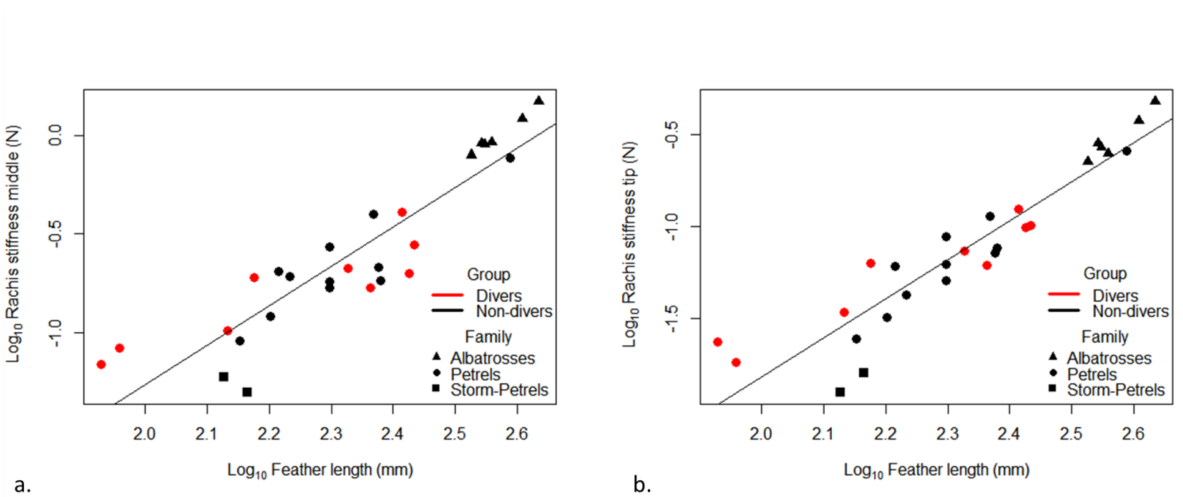


Figure 3.3. The relationship between the force required to bend P8 through an 8º angle of displacement from above (upstroke) and feather length among a group of procellariiform birds, a) middle (slope: 2.10 (95% CI 1.85-2.36) and intercept: -6.06 (95% CI -6.82- -5.29)) and b) tip (slope: 2.21 (95% CI 1.99-2.43) and intercept: -6.90 (95% CI -7.55- -6.25)).

Table 3.2: The allometric relationships between primary feather length and stiffness (force required to bend the feathers through an 8º arc from below = downstroke) among various groups of procellariform seabirds.

Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Non-divers	2.08 (1.74-2.43)	-6.43 (-7.45- -5.42)	0.95***
	Divers	1.77 (1.41-2.13)	-5.52 (-6.47- -4.48)	0.94***
	Procellariidae	1.89 (1.67-2.11)	-5.86 (-6.50- -5.22)	0.94***
	Procellariiformes	2.22 (2.02-2.41)	-6.81 (-7.40- -6.23)	0.95***
Middle	Non-divers	1.93 (1.60-2.26)	-5.53 (-6.50- -4.56)	0.95***
	Divers	1.61 (1.08-2.14)	-4.62 (-6.14- -3.11)	0.86***
	Procellariidae	1.75 (1.47-2.03)	-5.00 (-5.81- -4.19)	0.90***
	Procellariiformes	2.18 (1.94-2.42)	-6.24 (-6.95- -5.53)	0.93***
Base	Non-divers	1.57 (0.97-2.17)	-3.99 (-5.73- -2.24)	0.78***
	Divers	1.14 (0.31-1.96)	-2.77 (-5.14- -0.40)	0.55**
	Procellariidae	1.32 (0.88-1.77)	-3.28 (-4.57- -1.99)	0.67***
	Procellariiformes	2.02 (1.64-2.40)	-5.26 (-6.39- -4.12)	0.81***

*P<0.05 **P<0.01 ***P<0.001

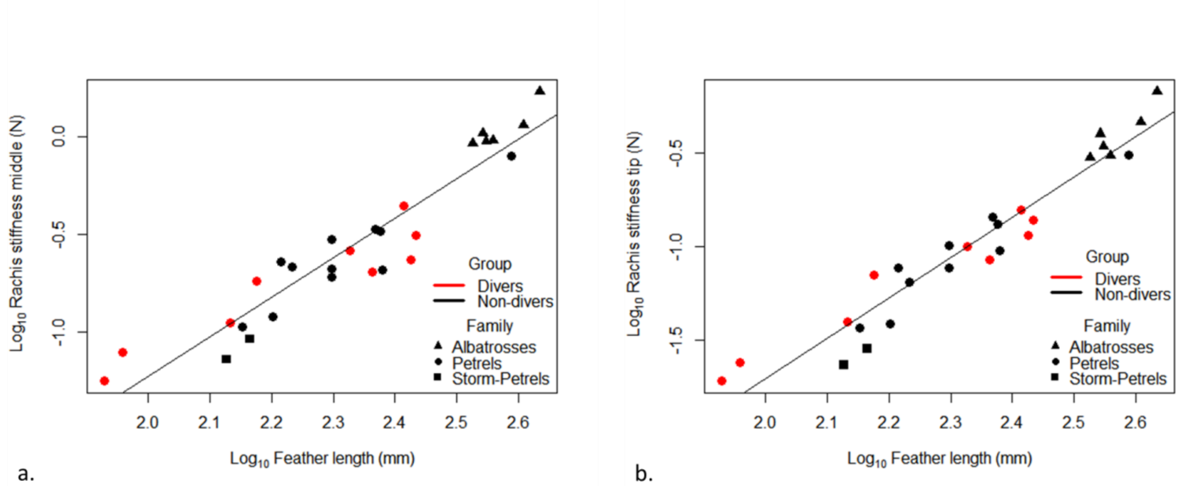


Figure 3.4. The relationship between the force required to bend P8 through 8º from below (downstroke) and feather length among a group of procellariiform birds, a) middle (slope: 2.18 (95% CI 1.94-2.42) and intercept: -6.24 (95% CI -6.95- -5.53)) and b) tip (slope: 2.22 (95% CI 2.02-2.41) and intercept: -6.81 (95% CI -7.40- -6.23)).

Table 3.3: The allometric relationships between primary feather stiffness and primary feather length in Procellariiformes (8º displacement from above, measured in the middle of the vane).

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.92 (1.28-2.56)	-4.48 (-5.80- -3.16)	0.82***
	Divers	2.33 (1.38-3.29)	-5.40 (-7.33- -3.47)	0.80***
	Procellariidae	2.17 (1.66-2.68)	-5.03 (-6.06- -3.99)	0.81***
	Procellariiformes	2.37 (2.05-2.68)	-5.43 (-6.09- -4.77)	0.90***
P4	Non-divers	1.88 (1.57-2.19)	-4.62 (-5.30- -.95)	0.95***
	Divers	1.67 (0.98-2.35)	-4.20 (-5.65- -2.75)	0.80***
	Procellariidae	1.77 (1.45-2.09)	-4.41 (-5.10- -3.72)	0.88***
	Procellariiformes	2.24 (1.95-2.53)	-5.39 (-6.02- -4.76)	0.90***
P6	Non-divers	1.85 (1.30-2.40)	-4.79 (-6.04- -3.54)	0.85***
	Divers	1.30 (0.71-1.89)	-3.61 (-4.91- -2.32)	0.77**
	Procellariidae	1.54 (1.17-1.90)	-4.10 (-4.91- -3.29)	0.80***
	Procellariiformes	2.15 (1.80-2.49)	-5.43 (-6.21- -4.64)	0.86***
P8	Non-divers	1.81 (1.03-2.58)	-4.84 (-6.63- -3.05)	0.73***
	Divers	1.13 (0.63-1.64)	-3.32 (-4.45- -2.20)	0.78**
	Procellariidae	1.36 (0.97-1.75)	-3.81 (-4.70- -2.93)	0.74***
	Procellariiformes	2.00 (1.64-2.36)	-5.26 (-6.12- -4.41)	0.82***
P10	Non-divers	2.06 (1.52-2.60)	-5.54 (-6.79- -4.29)	0.88***
	Divers	1.20 (0.94-1.45)	-3.55 (-4.11-2.98)	0.94***
	Procellariidae	1.45 (1.15-1.75)	-4.13 (-4.81- -3.44)	0.84***
	Procellariiformes	1.86 (1.62-2.11)	-5.05 (-5.61- -4.48)	0.90***

*P<0.05 **P<0.01 ***P<0.001

Table 3.4: The allometric relationships between primary feather stiffness and primary feather length in Procellariiformes (8º displacement from below, measured in the middle of the vane) for individual primaries.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.90 (1.45-2.35)	-4.39 (-5.31- -3.47)	0.90***
	Divers	2.54 (1.47-3.61)	-5.77 (-7.95- -3.60)	0.79***
	Procellariidae	2.26 (1.75-2.78)	-5.17 (-6.23- -4.12)	0.81***
	Procellariiformes	2.50 (2.17-2.84)	-5.68 (-6.37- -4.98)	0.90***
P4	Non-divers	1.96 (1.56-2.36)	-4.74 (-5.62- -3.86)	0.92***
	Divers	2.00 (1.20-2.79)	-4.87 (-6.56- -3.18)	0.81***
	Procellariidae	2.02 (1.64-2.40)	-4.89 (-5.71- -4.07)	0.87***
	Procellariiformes	2.45 (2.15-2.75)	-5.79 (-6.45- -5.13)	0.91***
P6	Non-divers	1.86 (1.40-2.32)	-4.76 (-5.81- -3.72)	0.89***
	Divers	1.39 (0.71-1.88)	-3.53 (-4.82- -2.24)	0.77**
	Procellariidae	1.53 (1.18-1.87)	-4.02 (-4.79- -3.26)	0.82***
	Procellariiformes	2.15 (1.81-2.49)	-5.39 (-6.15- -4.62)	0.86***
P8	Non-divers	1.79 (1.14-2.43)	-4.75 (-6.25- -3.26)	0.79***
	Divers	1.38 (0.94-1.83)	-3.86 (-4.85- -2.86)	0.87***

	Procellariidae	1.53 (1.21-1.85)	-4.17 (-4.90- -3.44)	0.84***
	Procellariiformes	2.03 (1.75-2.31)	-5.29 (-5.94- -4.63)	0.89***
P10	Non-divers	2.17 (1.69-2.65)	-5.77 (-6.88- -4.66)	0.91***
	Divers	1.18 (0.96-1.40)	-3.50 (-4.01- -3.00)	0.95***
	Procellariidae	1.48 (1.18-1.78)	-4.18 (-4.86- -3.49)	0.85***
	Procellariiformes	1.90 (1.65-2.15)	-5.09 (-5.68- -4.51)	0.90***

*P<0.05 **P<0.01 ***P<0.001

Table 3.5: The allometric relationships between primary feather stiffness and primary feather length in Procellariiformes (8º displacement from above, measured in the tip of the vane) for individual primaries.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.98 (1.29-2.66)	-5.09 (-6.51- -3.68)	0.80***
	Divers	2.53 (1.74-3.32)	-6.28 (-7.87- -4.68)	0.88***
	Procellariidae	2.28 (1.81-2.76)	-5.75 (-6.71- -4.79)	0.84***
	Procellariiformes	2.41 (2.08-2.74)	-6.03 (-6.71- -5.34)	0.89***
P4	Non-divers	2.12 (1.60-2.64)	-5.68 (-6.81- -4.54)	0.89***
	Divers	2.05 (1.63-2.46)	-5.51 (-6.40- -4.63)	0.94***
	Procellariidae	2.07 (1.80-2.35)	-5.57 (-6.17- -4.98)	0.93***
	Procellariiformes	2.40 (2.18-2.63)	-6.27 (-6.76- -5.77)	0.95***
P6	Non-divers	2.04 (1.60-2.48)	-5.73 (-6.73- -4.72)	0.91***
	Divers	1.58 (1.22-1.94)	-4.68 (-5.47- -3.89)	0.93***
	Procellariidae	1.74 (1.48-1.99)	-5.04 (-5.61- -4.47)	0.92***
	Procellariiformes	2.24 (1.96-2.51)	-6.13 (-6.76- -5.51)	0.91***
P8	Non-divers	2.15 (1.50-2.81)	-6.16 (-7.67- -5.51)	0.84***
	Divers	1.41 (1.00-1.82)	-4.41 (-5.33- -3.50)	0.89***
	Procellariidae	1.61 (1.26-1.96)	-4.88 (-5.68- -4.09)	0.83***
	Procellariiformes	2.13 (1.79-2.46)	-6.08 (-6.86- -5.29)	0.86***
P10	Non-divers	2.13 (1.62-2.64)	-6.22 (-7.39- -5.04)	0.90***
	Divers	1.56 (1.34-1.78)	-4.85 (-5.35- -4.36)	0.97***
	Procellariidae	1.71 (1.45-1.97)	-5.21 (-5.80- -4.62)	0.91***
	Procellariiformes	2.03 (1.83-2.23)	-5.94 (-6.41- -5.46)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Table 3.6: The allometric relationships between primary feather stiffness and primary feather length in Procellariiformes (8º displacement from below, measured in the tip of the vane) for individual primaries.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.99 (1.41-2.58)	-5.05 (-6.25- -3.86)	0.86***
	Divers	2.54 (1.73-3.34)	-6.21 (-7.84- -4.58)	0.87***
	Procellariidae	2.30 (1.85-2.74)	-5.70 (-6.61- -4.79)	0.86***
	Procellariiformes	2.47 (2.16-2.79)	-6.09 (-6.75- -5.42)	0.90***
P4	Non-divers	1.99 (1.57-2.42)	-5.28 (-6.20- -4.35)	0.92***
	Divers	2.04 (1.57-2.52)	-5.42 (-6.42- -4.41)	0.93***
	Procellariidae	2.04 (1.77-2.31)	-5.40 (-5.98- -4.82)	0.93***
	Procellariiformes	2.36 (2.14-2.58)	-6.08 (-6.56- -5.60)	0.95***
P6	Non-divers	2.04 (1.69-2.40)	-5.60 (-6.40- -4.79)	0.94***
	Divers	1.63 (1.24-2.02)	-4.69 (-5.54- -3.84)	0.92***
	Procellariidae	1.79 (1.55-2.03)	-5.04 (-5.57- -4.51)	0.93***
	Procellariiformes	2.25 (2.00-2.50)	-6.05 (-5.57- -4.51)	0.93***
P8	Non-divers	2.06 (1.51-2.60)	-5.81 (-7.07- -4.55)	0.88***
	Divers	1.64 (1.30-1.97)	-4.84 (-5.59- -4.09)	0.94***
	Procellariidae	1.76 (1.50-2.03)	-5.13 (-5.73- -4.53)	0.91***
	Procellariiformes	2.16 (1.92-2.41)	-6.04 (-6.61- -5.47)	0.93***
P10	Non-divers	2.32 (1.97-2.67)	-6.58 (-7.38- -5.78)	0.96***
	Divers	1.35 (1.12-1.58)	-4.31 (-4.83- -3.78)	0.96***
	Procellariidae	1.62 (1.33-1.90)	-4.94 (-5.59- -4.28)	0.88***
	Procellariiformes	1.97 (1.75-2.19)	-5.71 (-6.23- -5.20)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Feather stiffness relative to body mass

The geometric similarity theory predicts that the scaling relationship for stiffness relative to body mass to be 1.67 for isometry (Worcester 1996). However, my results for all three measures of flexure (4º, 8 º (Tables 3.7 and 3.8), and 12º) and at all three feather locations (base, middle and tip) showed strong negative allometry. There were no significant differences along the vane and among the different degrees between diving and non-diving birds (Appendix 26a-28). The primaries of birds that tend to use their wings for underwater propulsion were less stiff relative to body size than birds that do not use their wings for underwater propulsion (Figures 3.5 and 3.6).

Table 3.7: The allometric relationships between primary feather stiffness and primary feather mass in Procellariiformes (8º displacement from above).

Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Non-divers	0.63 (0.48-0.78)	-2.06 (-2.45- -1.66)	0.90***
	Divers	0.78 (0.60-0.95)	-2.62 (-3.10- -2.14)	0.93***
	Procellariidae	0.67 (0.52-0.82)	-2.24 (-2.63- -1.86)	0.83***
	Procellariiformes	0.67 (0.60-0.74)	-2.22 (-2.42- -2.01)	0.93***
Middle	Non-divers	0.58 (0.45-0.71)	-1.42 (-1.76- -1.08)	0.91***
	Divers	0.64 (0.40-0.89)	-1.78 (-2.44- -1.11)	0.83***
	Procellariidae	0.58 (0.42-0.74)	-1.51 (-1.93- -1.09)	0.76***
	Procellariiformes	0.63 (0.55-0.72)	-1.61 (-1.85- -1.38)	0.90***
Base	Non-divers	0.47 (0.27-0.68)	-0.63 (-1.17- -0.10)	0.73***
	Divers	0.46 (0.13-0.78)	-0.75 (-1.64- -0.13)	0.56**
	Procellariidae	0.44 (0.26-0.63)	-0.62 (-1.12- -0.13)	0.56**
	Procellariiformes	0.57 (0.46-0.69)	-0.91 (-1.23- -0.58)	0.80***

*P<0.05 **P<0.01 ***P<0.001

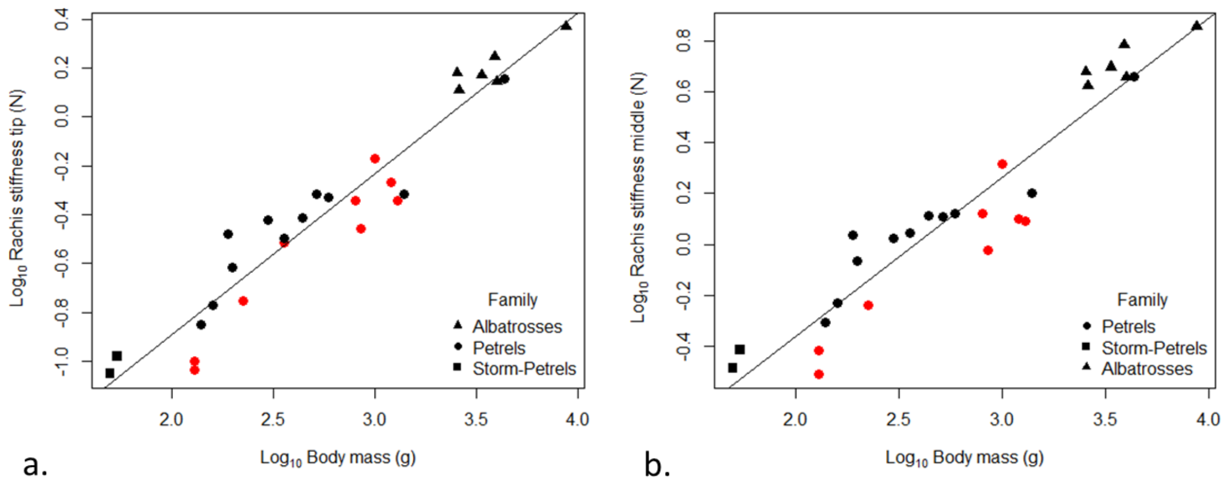


Figure 3.5. The influence of diving behaviour on the relationship between primary body mass and feather stiffness during the upstroke at a) the middle (slope: 0.63 (95% CI 0.55-0.72) and intercept: -1.61 (95% CI -1.85- -1.38)) and b) tip (slope: 0.67 (95% CI 0.60-0.74) and intercept: -2.22 (95% CI -2.42- -2.01)) of all ten primary feathers among Procellariiformes (red = divers; black = non-diving species).

Table 3.8: The allometric relationships between primary feather stiffness and primary feather mass in Procellariiformes (8° displacement from below).

Section	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Non-divers	0.62 (0.51-0.74)	-1.94 (-2.24- -1.64)	0.94***
	Divers	0.78 (0.59-0.98)	-2.55 (-3.09- -2.02)	0.92***
	Procellariidae	0.67 (0.52-0.82)	-2.14 (-2.55- -2.02)	0.82***
	Procellariiformes	0.66 (0.59-0.74)	-2.11 (-2.32- -1.89)	0.92***
Middle	Non-divers	0.58 (0.48-0.68)	-1.38 (-1.64- -1.11)	0.94***
	Divers	0.71 (0.45-0.97)	-1.92 (-2.63- -1.21)	0.83***
	Procellariidae	0.61 (0.44-0.78)	-1.54 (-1.98- -1.10)	0.76**
	Procellariiformes	0.65 (0.56-0.74)	-1.61 (-1.86- -1.37)	0.90***
Base	Non-divers	0.48 (0.32-0.64)	-0.64 (-1.06- -0.21)	0.82***
	Divers	0.49 (0.10-0.88)	-0.83 (-1.89- -0.23)	0.50*
	Procellariidae	0.46 (0.27-0.66)	-0.66 (-1.18- -0.14)	0.56*
	Procellariiformes	0.61 (0.49-0.73)	-0.98 (-1.32- -0.64)	0.80***

*P<0.05 **P<0.01 ***P<0.001

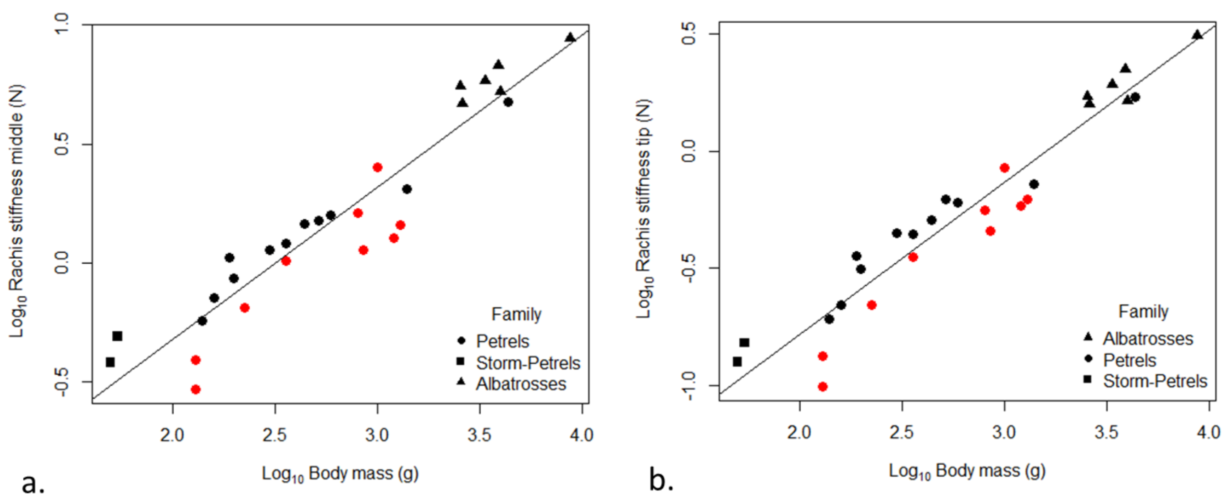


Figure 3.6. The influence of diving behaviour on the relationship between primary body mass and rachis stiffness during the downstroke at a) the middle (slope: 0.65 (95% CI 0.56-0.74) and intercept: -1.61 (95% CI -1.86- -1.37)) and b) tip (slope: 0.66 (95% CI 0.59-0.74) and intercept: -2.11 (95% CI -2.32- -1.89)of all ten primary feathers among Procellariform seabirds (red = divers; black = non- diving species).

Relative stiffness along the vane

The force required to bend a feather through a fixed angle is invariably less when the force is applied farther from the point of attachment (the feather base). To test whether the rate at which the force decreased with distance from the base varied between divers and non-divers, I explored the proportion of force required to bend the middle and tip of the feather relative to that at the base (as well as the tip relative to the middle of the vane). These proportions appear to be largely independent of feather length or body size (Figure 3.7), and so I was able to directly compare the proportions between groups of birds. Differences were subtle, but on average diving birds showed less decrease in force compared to non-diving birds, suggesting that their feathers are slightly stiffer (Figures 3.8 – 3.10).

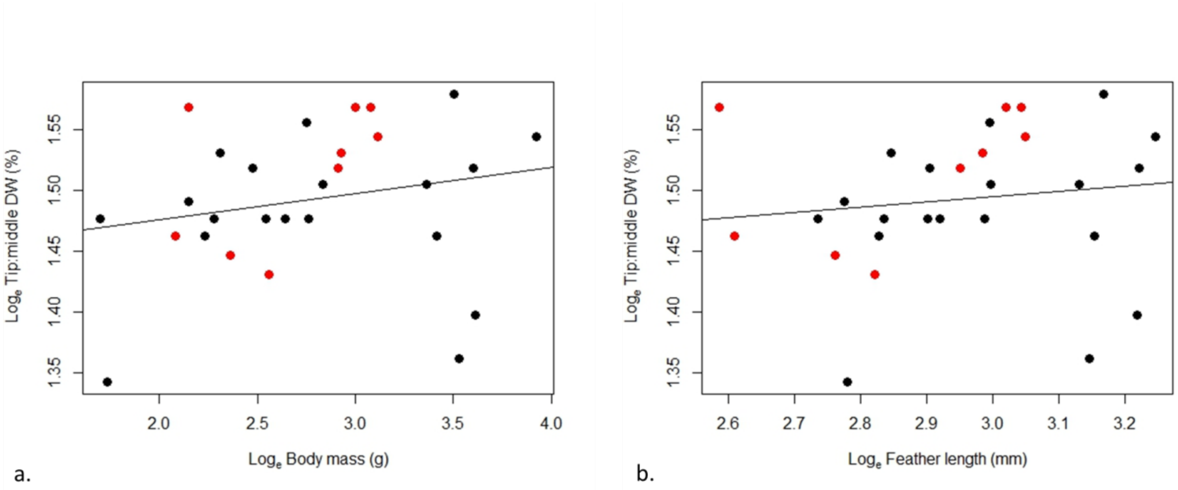


Figure 3.7 The proportion of force required to bend the feather relative to body mass (a) and feather length (b). Feathers from both the diving (red) and non-diving (black) petrels show that they are not dependent on the body mass and feather length. The regression line shows no significant differences between the two groups.

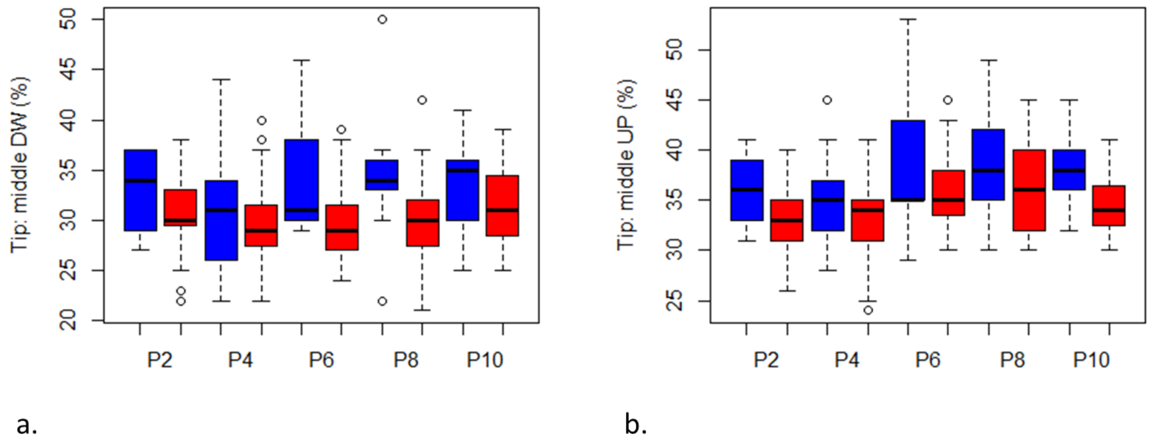


Figure 3.8. The force required to bend the tip relative to the middle of the feather of 33 species of Procellariiformes showing that divers (blue) average slightly greater than non-divers (red); the ratios between tip and middle averaged slightly less on the downstroke (a) than on the upstroke (b).

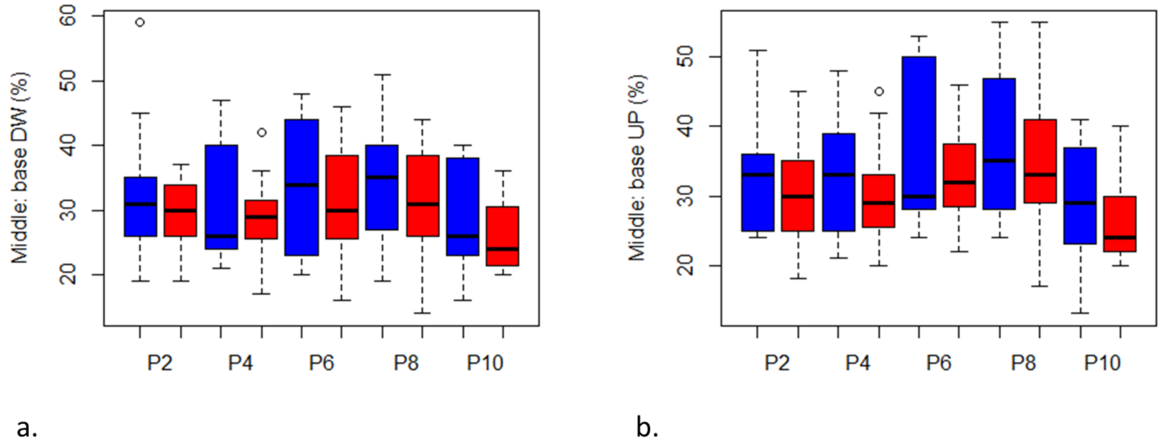
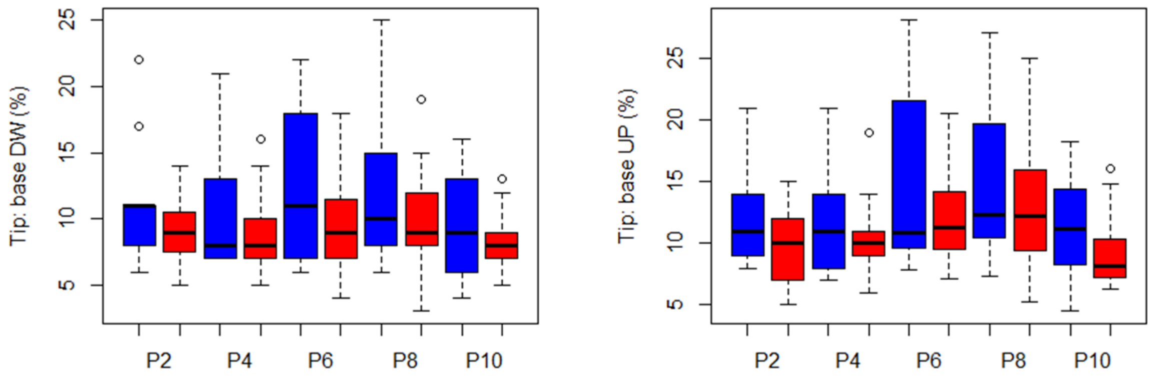


Figure 3.9. The force required to bend the middle relative to the base of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b).



a. b.

Figure 3.10. The force required to bend the tip relative to the base of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b).

DISCUSSION

The rachis bears most of the forces to which flight feathers are subjected as they push the bird forward, and they accommodate these forces to some extent by bending. Because water is much denser than air, I expected birds that use their wings for underwater propulsion as well as flight to have stronger, deeper rachises, given that flight feather flexibility is positively correlated with rachis diameter or depth (Worcester 1996; Wang *et al*. 2012; Pap *et al*. 2013).

Generating lift and thrust is an essential role played by flight feathers during flight in air, and the forces generated are transferred to the skeleton via the wing bones. The forces experienced during flight can be considerable and require not only strong bones but strong feathers. Bird size also plays an important role in terms of the magnitude of lift and thrust forces experienced by the wing feathers; large birds experience greater forces because of the greater surface area of their wings (Worcester 1996). Feathers of large birds are more flexible than those of small birds (Worcester 1996; Pap *et al*. 2013), apparently to reduce the stress of flight on the wing skeleton (Worcester 1996). However, I found a lot of noise in the data on rachis depth, confounding attempts to detect consistent patterns related to whether petrels fly underwater or not.

The outer primaries face greater forces than the inner primaries because they move more rapidly through the air/water and form the leading edge of the wing which needs to be strong and rigid (Ennos *et al*. 1995). Also, in general, less of the outer primaries length is protected by the coverts. The wing functions as a unit but I measured feather stiffness on individual feathers, this is because wing feathers experience forces differently along the wing. Therefore, I expected differences between the divers and non-divers to be more marked on the outer feathers (Corning and Biewener 1998). Although most birds have stiffer outer primaries compared to the inner primaries, the primaries of diving birds have additional hydrodynamic roles which might require them to be even stiffer than in non-diving birds. However, no strong signal was found as evidence to show that the individual primary feathers of diving birds were stiffer than the primary feathers of the non-diving birds. Stiff feathers are more vulnerable to mechanical damage during strong forces that can be experienced in air and especially under water compared to feathers that are flexible (Pennycuick 1987b; Worcester 1996; Wang *et al.* 2012). Diving birds need to have stiff feathers to avoid damage to their feathers when they perform their flights in different media.

Feather length greatly affected the force measurements. Short feathers require more force to bend through a given angle, partly because of the congestion of the 'foam' (white substance) found in the rachis, but mainly because the force is spread over a shorter length of feather (Vincent 1990; Alexander 1985). As with previous studies (Worcester 1996; Wang *et al.* 2012), I found there was a negative allometry between feather stiffness and body mass. Diving birds tended to lie below the regression line, which may be a consequence of their short feathers. Birds with large bodies have to be able to lift their bodies using the strength from the feathers; most of the non-diving birds have larger bodies compared to the diving birds. Strong feathers are a prerequisite to be able to lift and maintain big bodies in air and in a much denser medium such as water.

The force required to bend the outer primaries was generally less than the inner primaries, which is counter-intuitive, because outer primaries are expected to be stiffer given their faster movement through the air, and the need to reinforce the leading edge of the wing. However, the outer primaries are also longer, and the longer the moment of arc, the less the force required to bend through a fixed angle, and this plays a bigger role than location on the wing. The effect of feather length is less marked in birds with rounded wings, because the primaries are less varied in length, and indeed the outer primaries are shorter than P7-8 (Dawson 2005), but this does not apply to any procellariform birds. As expected, the forces required to bend the feather through a fixed angle were greater at the base of the vane than at the middle and tip, due to the shorter moment of arc as well as the thicker rachis at the base. The force required to bend feathers from below (upstroke) was always slightly greater than from above, which also is counter-intuitive because wings might be expected to experience greater aerodynamic forces on the power-generating downstroke than the upstroke. The difference probably results from the natural curvature of flight feathers (especially the primaries), which curve down towards the tip. The proportional decrease in force required to effect a fixed magnitude of deflection averaged less among diving birds than non-diving petrels, which indicates a tendency towards greater rigidity along the feather in diving birds. However, the data were noisy, with considerable variation between species.

CONCLUSIONS

I expected that the feathers of petrels that use their wings for propulsion underwater would be deeper and stiffer compared to those of closely related species that do not use their wings underwater because of the dense nature of water. However, there was little evidence that this was the case, even among the outer primaries that are exposed to the greatest forces during flight. There also was no clear pattern in rachis depth, which correlates with feather stiffness. I conclude that by partly folding the wing to further reduce wing area during underwater ‘flight’, the increased overlap between wing feathers is sufficient to create an effective paddle to allow petrels to ‘fly’ underwater.

CHAPTER 4: SYNTHESIS AND CONCLUSIONS

The adaptations of wing-propelled divers have been studied in terms of physiology, behaviour and wing morphology (Raikow *et al.* 1988), but feather adaptations have largely been ignored. This thesis investigated whether the flight feathers of petrels that manage to utilise the same wing to 'fly' in two very different media, air and water, differ from those that seldom if ever dive. Procellariiformes were the focus of the study because they are the only order of birds that exhibit a wide range of wing- propelled diving behaviour. However, the challenge with this order is the wide range of body size. Albatrosses and diving petrels differ significantly in terms of body mass, so I used allometric techniques to control for the effect of body mass.

The wings of wing-propelled divers are relatively short compared to petrels that only use their wings for flight in air (Kuroda 1654; 1967). Short wings are advantageous underwater because they minimise drag, but short-winged birds generally need to flap frequently during aerial flight to remain airborne, greatly increasing the energetic costs of flight compared to non-diving petrels and albatrosses. The flight feathers of petrels and shearwaters that routinely dive underwater greater than 10 m were found to be shorter than those of the non-diving birds. This difference was more marked in the smaller divers (diving petrels, *Puffinus* shearwaters) than larger diving species (*Ardenna* shearwaters and *Procellaria* petrels), and was most obvious in the primary feathers – especially the outer primaries.

Feather microstructure did not show any marked differences between the two groups. Feather depth and barb length showed minimal differences statistically, but divers tend to have vanes that are broader than non-diving birds, possibly a consequence of having shorter feathers. There was also a lot of noise in these data, making it hard to detect clear patterns in the data.

There is some evidence that diving birds have slightly stiffer flight feathers compared to non-diving petrels, with the forces required to bend the different sections along the vane consistently being slightly greater than those of the non-diving birds, supporting the expectation that diving birds have stiffer feathers. Negative allometry was found when scaling feather stiffness with body mass, similar to the results obtained by Worcester (1996) and Wang *et al*. (2012).

Diving birds appear to have invested primarily in evolving short wings and as a result evolved stiff feathers to be able to use their wings underwater. Both these adaptations allow their wings to function underwater with minimal risk of mechanical damage. However, the difference in stiffness was less than expected, given the much greater density of water than air. Wing-propelled diving birds probably obtain most wing rigidity necessary for underwater flapping by partly closing the wing, creating additional overlap between adjacent feathers. By comparison, in aerial flight they spread the individual feathers to generate lift and propulsion.

A broader study might compare the feathers of wing-propelled divers, foot-propelled divers and plunge divers to see whether they differ in terms of allometry, structure and rigidity. Tail feathers may also be added to the study to see whether they show different allometric relationships compared to wing and body feathers (Pap *et al.* 2016). Mechanical properties, such as the foam found in the rachis core may also be tested to see how much they contribute towards the stiffness of the feathers. This thesis adds to the limited knowledge about the variability of feathers from different groups of birds.

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APPENDICES

Appendix 1: The number of secondaries in Procellariiformes that use their wings underwater (represented by an asterisk) and those that do not.

Family	Genus	Body mass	Secondaries	Sources
Oceanitidae				
	Oceanites	34-45 g	11	Marchant and Higgins 1990; Del Hoyo *et al.* 1992
	Garrodia	34 g		Marchant and Higgins 1990; Del Hoyo *et al.* 1992
	Pelagodroma	60 g		Marchant and Higgins 1990; Del Hoyo *et al.* 1992
	Fregetta	50-60 g	12-13	Marchant and Higgins 1990; Del Hoyo *et al.* 1992
	Nesofregetta			
Diomedeidae				
	Phoebastria	2300-3600 g		Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Diomedea	4800-11300 g	34	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	*Phoebetria**	2400-3100 g	24	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Thalassarche	2400-5000 g	26-28	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
Hydrobatidae				
	Hydrobates	23-29 g		Marchant and Higgins 1990; Del Hoyo *et al.* 1992
	Oceanodroma	29-59 g	14	Marchant and Higgins 1990; Del Hoyo *et al.* 1992
Procellariidae				
	Macronectes	3800-5000 g	28	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Fulmarus	700-835 g	21	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Thalassoica	510-765 g	24	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Daption	340-380 g	19	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Pagodroma	240-460 g	16	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Halobaena	170-230 g	16	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005

	Pachyptila	90-235 g	15-18	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Aphrodroma	331-357 g	18-20	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Pterodroma	140-810 g	15-24	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Pseudobulweria	160-270 g		Harrison 1983; Marchant and Higgins 1990; Hockey *et al*. 2005; Safford and Hawkins 2013
	*Procellaria**	680-1420 g	22-24	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	*Calonectris**	440-956 g	20	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	*Ardenna**	300-978 g	20-22	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	*Puffinus**	150-525 g	19-20	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	*Pelecanoides**	86-185 g	12	Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005
	Bulweria	78-130 g		Harrison 1983; Marchant and Higgins 1990; Del Hoyo *et al.* 1992; Hockey *et al*. 2005

Appendix 2: The slope comparison of primaries and secondaries between divers and non-divers.

	Sum Sq	Mean Sq	F-value	Pr (>F)
Total flight feather length relative to body mass				
Body mass	<0,001	<0,001	0,292	0,593
Group	<0,001	<0,001	0,101	0,753
Bodymass:Group	<0,001	<0,001	0,002	0,968
Total flight feather mass relative to body mass				
Body mass	<0,001	<0,001	0,025	0,875
Group	<0,001	<0,001	0	0,999
Bodymass:Group	<0,001	<0,001	0,002	0,659
Primary feather length relative to body mass				
Body mass	<0,001	<0,001	3,104	0,0886
Group	<0,001	<0,001	3,352	0,1359
Bodymass:Group	<0,001	<0,001	0,174	0,6793
Primary feather mass relative to body mass				
Body mass	<0,001	<0,001	0,676	0,4177
Group	<0,001	<0,001	0,011	0,9176
Bodymass:Group	<0,001	<0,001	2,967	0,0956
Primary feather mass relative to primary feather length				
Body mass	<0,001	<0,001	8,889	0,00576
Group	<0,001	<0,001	0,849	0,36455
Bodymass:Group	<0,001	<0,001	10,182	0,0034
Secondary feather length relative to body mass				
Body mass	85788362	85788362	259,541	<0,001
Group	6565	6565	0,02	0,88889
Bodymass:Group	1949186	1949186	5,897	0,0218
Secondary feather mass relative to body mass				
Body mass	478974159	478974159	56,843	<0,001
Group	7120785	7120785	0,845	0,366
Bodymass:Group	142489	142489	0,017	0,897
Secondary feather mass relative to secondary feather length				
Body mass	476238208	476238208	57,669	<0,001
Group	7895449	7895449	0,956	0,337
Bodymass:Group	6812173	6812173	0,825	

Appendix 3a: The allometric relationship between primary feather length and vane width at the base of the feather for all 20 Procellariidae.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.80 (0.64-0.95)	0.11 (-0.21-0.43)	0.93***
	Divers	1.04 (0.82-1.26)	-0.34 (-0.77-0.10)	0.94***
	Procellariidae	0.90 (0.76-1.04)	-0.08 (-0.37-0.20)	0.90***
P2	Non-divers	0.79 (0.66-0.93)	0.08 (-0.20-0.36)	0.94***
	Divers	0.96 (0.77-1.15)	-0.23 (-0.62-0.15)	0.95***
	Procellariidae	0.86 (0.74-0.98)	-0.05 (-0.30-0.19)	0.92***
P3	Non-divers	0.83 (0.72-0.93)	-0.03 (-0.25-0.19)	0.97***
	Divers	0.87 (0.67-1.07)	-0.10 (-0.51-0.31)	0.93***
	Procellariidae	0.86 (0.73-0.94)	-0.05 (-0.25-0.19)	0.92***
P4	Non-divers	0.86 (0.76-0.96)	-0.15 (-0.37-0.07)	0.97***
	Divers	0.81 (0.68-0.94)	0.00 (-0.28-0.28)	0.96***
	Procellariidae	0.81 (0.71-0.90)	-0.01 (-0.21-0.19)	0.95***
P5	Non-divers	0.88 (0.79-0.98)	-0.22 (-0.43- -0.01)	0.98***
	Divers	0.80 (0.69-0.91)	0.00 (-0.23-0.23)	0.97***
	Procellariidae	0.81 (0.72-0.89)	-0.04 (-0.23-0.15)	0.95***
P6	Non-divers	0.92 (0.82-1.01)	-0.32 (-0.54- -0.10)	0.98***
	Divers	0.76 (0.65-0.87)	0.06 (-0.18-0.31)	0.97***
	Procellariidae	0.79 (0.70-0.88)	-0.03 (-0.22-0.17)	0.95***
P7	Non-divers	0.92 (0.79-1.05)	-0.36 (-0.65- -0.65)	0.96***
	Divers	0.73 (0.58-0.87)	0.11 (-0.21-0.42)	0.95***
	Procellariidae	0.77 (0.67-0.87)	0.00 (-0.22-0.23)	0.93***
P8	Non-divers	0.82 (0.70-0.95)	-0.17 (-0.46-0.12)	0.96***
	Divers	0.74 (0.65-0.84)	0.04 (-0.17-0.25)	0.98***
	Procellariidae	0.75 (0.67-0.83)	0.01 (-0.17-0.19)	0.95***
P9	Non-divers	0.85 (0.72-0.99)	-0.28 (-0.59-0.03)	0.95***
	Divers	0.69 (0.58-0.79)	0.14 (-0.10-0.38)	0.97***
	Procellariidae	0.72 (0.62-0.81)	0.05 (-0.16-0.27)	0.93***
P10	Non-divers	0.77 (0.59-0.94)	-0.06 (-0.46-0.34)	0.91***
	Divers	0.67 (0.58-0.76)	0.17 (-0.03-0.37)	0.98***
	Procellariidae	0.69 (0.61-0.78)	0.11 (-0.07-0.30)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Appendix 3b: The allometric relationship between secondary feather length and vane width at the base of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.78 (0.60-0.95)	0.18 (-0.17-0.53)	0.91***
	Divers	0.95 (0.86-1.05)	-0.14 (-0.32-0.04)	0.99***
	Procellariidae	0.86 (0.75-0.97)	0.02 (-0.19-0.24)	0.94***
S2	Non-divers	0.74 (0.54-0.95)	0.25 (-0.15-0.66)	0.87***
	Divers	0.84 (0.74-0.93)	0.10 (-0.09-0.28)	0.99***
	Procellariidae	0.78 (0.67-0.89)	0.19 (-0.02-0.40)	0.93***
S3	Non-divers	0.72 (0.49-0.95)	0.29 (-0.15-0.74)	0.83***
	Divers	0.84 (0.71-0.97)	0.10 (-0.15-0.34)	0.97***
	Procellariidae	0.76 (0.62-0.89)	0.23 (-0.04-0.50)	0.88***
S4	Non-divers	0.97 (0.73-1.20)	-0.18 (0.65-0.29)	0.89***
	Divers	0.79 (0.70-0.88)	0.20 (0.02-0.37)	0.98***
	Procellariidae	0.83 (0.69-0.96)	0.11 (-0.16-0.38)	0.90***
S5	Non-divers	0.75 (0.51-1.00)	0.22 (-0.26-0.69)	0.83***
	Divers	0.71 (0.64-0.78)	0.33 (0.20-0.47)	0.99***
	Procellariidae	0.70 (0.56-0.83)	0.34 (0.20-0.47)	0.87***
S6	Non-divers	0.79 (0.60-0.99)	0.14 (-0.24-0.52)	0.87***
	Divers	0.67 (0.58-0.76)	0.42 (0.24-0.61)	0.89***
	Procellariidae	0.68 (0.55-0.81)	0.38 (0.12-0.63)	0.98***
S7	Non-divers	0.76 (0.56-0.97)	0.21 (-0.19-0.61)	0.87***
	Divers	0.63 (0.56-0.70)	0.49 (0.36-0.63)	0.99***
	Procellariidae	0.68 (0.55-0.81)	0.44 (0.22-0.66)	0.89***
S8	Non-divers	0.74 (0.51-0.97)	0.26 (-0.19-0.72)	0.84***
	Divers	0.61 (0.50-0.72)	0.55 (0.33-0.76)	0.96***
	Procellariidae	0.62 (0.49-0.75)	0.50 (0.25-0.76)	0.85***
S9	Non-divers	0.76 (0.52-1.00)	0.22 (-0.25-0.70)	0.83***
	Divers	0.59 (0.50-0.67)	0.59 (0.42-0.75)	0.98***
	Procellariidae	0.62 (0.49-0.75)	0.50 (0.28-0.73)	0.88***
S10	Non-divers	0.73 (0.55-0.91)	0.28 (-0.07-0.63)	0.90***
	Divers	0.61 (0.50-0.71)	0.56 (0.36-0.77)	0.96***
	Procellariidae	0.61 (0.51-0.72)	0.53 (0.32-0.73)	0.89***

*P<0.05 **P<0.01 ***P<0.001

Appendix 4a: The allometric relationship between primary feather length and vane width at the middle of the feather.

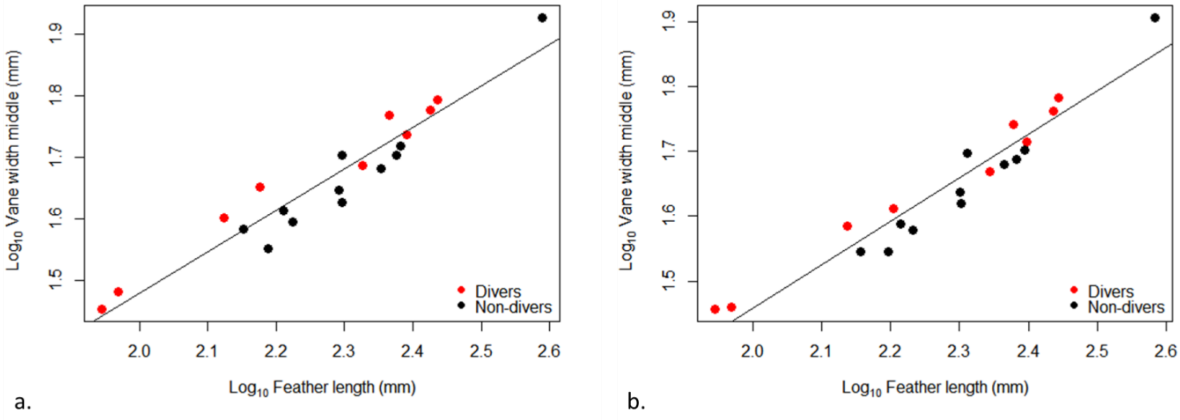
Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.78 (0.67-0.88)	0.13 (-0.08-0.33)	0.97***
	Divers	0.97 (0.77-1.17)	-0.25 (-0.64-0.15)	0.94***
	Procellariidae	0.86 (0.75-0.95)	-0.04 (-0.27-0.20)	0.93***
P2	Non-divers	0.76 (0.58-0.94)	0.11 (-0.26-0.49)	0.90***
	Divers	0.86 (0.66-1.05)	-0.05 (-0.45-0.34)	0.93***
	Procellariidae	0.79 (0.67-0.72)	0.06 (-0.20-0.31)	0.90***
P3	Non-divers	0.80 (0.71-0.89)	-0.01 (-0.21-0.18)	0.97***
	Divers	0.80 (0.65-0.95)	0.02 (-0.29-0.33)	0.95***
	Procellariidae	0.78 (0.69-0.87)	0.04 (-0.15-0.24)	0.94***
P4	Non-divers	0.82 (0.72-0.92)	-0.09 (-0.31-0.13)	0.97***
	Divers	0.75 (0.59-0.90)	0.11 (-0.22-0.44)	0.94***
	Procellariidae	0.75 (0.65-0.85)	0.08 (-0.14-0.29)	0.93***
P5	Non-divers	0.82 (0.67-0.98)	-0.12 (-0.47-0.22)	0.93***
	Divers	0.72 (0.62-0.80)	0.15 (-0.03-0.34)	0.98***
	Procellariidae	0.73 (0.63-0.83)	0.10 (-0.12-0.33)	0.92***
P6	Non-divers	0.82 (0.66-0.97)	-0.14 (-0.49-0.20)	0.94***
	Divers	0.69 (0.60-0.78)	0.17 (-0.03-0.37)	0.98***
	Procellariidae	0.73 (0.61-0.81)	0.10 (-0.10-0.34)	0.92***
P7	Non-divers	0.87 (0.70-1.04)	-0.30 (-0.68-0.09)	0.93***
	Divers	0.65 (0.52-0.79)	0.23 (-0.06-0.53)	0.94***
	Procellariidae	0.69 (0.58-0.81)	0.12 (-0.13-0.38)	0.90***
P8	Non-divers	0.81 (0.64-0.98)	-0.20 (-0.60-0.20)	0.92***
	Divers	0.65 (0.55-0.75)	0.21 (-0.02-0.43)	0.97***
	Procellariidae	0.68 (0.57-0.78)	0.13 (-0.11-0.37)	0.90***
P9	Non-divers	0.84 (0.69-0.99)	-0.28 (-0.63-0.07)	0.94***
	Divers	0.62 (0.54-0.70)	0.24 (0.06-0.42)	0.98***
	Procellariidae	0.67 (0.57-0.77)	0.12 (-0.10-0.34)	0.92***
P10	Non-divers	0.68 (0.51-0.86)	0.10 (-0.31-0.30)	0.88***
	Divers	0.65 (0.56-0.75)	0.19 (-0.02-0.40)	0.97***
	Procellariidae	0.65 (0.56-0.73)	0.19 (-0.01-0.39)	0.93***

*P<0.05 **P<0.01 ***P<0.001

Appendix 4b: The allometric relationship between secondary feather length and vane width at the middle of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.75 (0.58-0.91)	0.25 (-0.07-0.58)	0.91***
	Divers	0.82 (0.75-0.88)	0.13 (0.01-0.26)	0.99***
	Procellariidae	0.78 (0.69-0.86)	0.20 (0.04-0.37)	0.96***
S2	Non-divers	0.76 (0.52-1.00)	0.26 (-0.22-0.73)	0.83***
	Divers	0.81 (0.71-0.91)	0.16 (-0.03-0.35)	0.98***
	Procellariidae	0.78 (0.67-0.89)	0.21 (-0.01-0.43)	0.92***
S3	Non-divers	0.66 (0.39-0.93)	0.45 (-0.07-0.98)	0.75***
	Divers	0.84 (0.73-0.95)	0.12 (-0.09-0.32)	0.98***
	Procellariidae	0.76 (0.64-0.89)	0.26 (0.01-0.51)	0.90***
S4	Non-divers	0.85 (0.58-1.13)	0.09 (-0.45-0.63)	0.83***
	Divers	0.83 (0.78-0.89)	0.13 (0.02-0.24)	0.99***
	Procellariidae	0.84 (0.72-0.95)	0.13 (-0.10-0.35)	0.93***
S5	Non-divers	0.73 (0.50-0.96)	0.33 (-0.12-0.79)	0.83***
	Divers	0.85 (0.77-0.91)	0.11 (-0.01-0.35)	0.99***
	Procellariidae	0.79 (0.69-0.90)	0.20 (0.00-0.41)	0.93***
S6	Non-divers	0.72 (0.49-0.94)	0.35 (-0.09-0.80)	0.83***
	Divers	0.83 (0.76-0.91)	0.14 (-0.01-0.29)	0.99***
	Procellariidae	0.78 (0.68-0.89)	0.23 (0.03-0.44)	0.93***
S7	Non-divers	0.72 (0.48-0.97)	0.34 (-0.15-0.82)	0.81***
	Divers	0.81 (0.73-0.88)	0.19 (0.06-0.33)	0.99***
	Procellariidae	0.77 (0.66-0.88)	0.26 (0.05-0.46)	0.93***
S8	Non-divers	0.74 (0.60-0.98)	0.31 (-0.13-0.75)	0.83***
	Divers	0.86 (0.72-1.00)	0.09 (-0.18-0.35)	0.97***
	Procellariidae	0.81 (0.70-0.92)	0.17(-0.05-0.39))	0.93***
S9	Non-divers	0.74 (0.52-0.96)	0.31 (-0.13-0.75)	0.85***
	Divers	0.82 (0.73-0.90)	0.17 (0.01-0.33)	0.99***
	Procellariidae	0.79 (0.69-0.88)	0.22 (0.04-0.41)	0.95***
S10	Non-divers	0.72 (0.48-0.96)	0.35 (-0.12-0.83)	0.82***
	Divers	0.82 (0.71-0.94)	0.16 (-0.05-0.37)	0.98***
	Procellariidae	0.78 (0.68-0.89)	0.23 (0.03-0.43)	0.93***

*P<0.05 **P<0.01 ***P<0.001



Appendix 4c: The distal primary feathers a) P8 (slope: 0.68 (95% CI 0.57-0.78) and intercept: 0.13 (95% CI -0.11-0.37)) and b) P9 (slope: 0.67 (95% CI 0.57-0.77) and intercept: 0.12 (95% CI -0.10-0.34)) showing how vane width in the middle of the outer primaries of underwater divers are broader relative to feather length compared to petrels that do not dive underwater.

Appendix 5a: The allometric relationship between primary feather length and vane width at the tip of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.82 (0.72-0.92)	-0.09 (-0.29-0.112)	0.97***
	Divers	0.88 (0.63-1.13)	-0.20 (-0.70-0.30)	0.89***
	Procellariidae	0.84 (0.73-0.95)	-0.14(-0.55-0.20)	0.93***
P2	Non-divers	0.78 (0.66-0.90)	-0.06 (-0.30-0.18)	0.96***
	Divers	0.85 (0.64-1.05)	-0.17 (-0.60-0.25)	0.92***
	Procellariidae	0.80 (0.70-0.91)	-0.10 (-0.31-0.11)	0.93***
P3	Non-divers	0.74 (0.64-0.84)	-0.01 (-0.23-0.20)	0.96***
	Divers	0.78 (0.63-0.93)	-0.07 (-0.38-0.24)	0.95***
	Procellariidae	0.75 (0.66-0.84)	-0.01 (-0.20-0.18)	0.94***
P4	Non-divers	0.76 (0.62-0.90)	-0.09 (-0.39-0.21)	0.94***
	Divers	0.72 (0.60-0.84)	0.03 (-0.22-0.28)	0.96***
	Procellariidae	0.71 (0.62-0.81)	0.03 (-0.18-0.23)	0.93***
P5	Non-divers	0.76 (0.62-0.90)	-0.10 (-0.41-0.21)	0.94***
	Divers	0.75 (0.63-0.86)	-0.04 (-0.30-0.22)	0.97***
	Procellariidae	0.73 (0.65-0.82)	-0.03 (-0.22-0.16)	0.94***
P6	Non-divers	0.81 (0.66-0.96)	-0.24 (-0.58-0.10)	0.94***
	Divers	0.71 (0.60-0.82)	0.02 (-0.22-0.27)	0.97***
	Procellariidae	0.73 (0.63-0.83)	-0.03 (-0.23-0.17)	0.94***
P7	Non-divers	0.84 (0.69-1.00)	-0.32 (-0.67-0.04)	0.94***
	Divers	0.70 (0.55-0.85)	0.02 (-0.31-0.36)	0.94***
	Procellariidae	0.73 (0.63-0.83)	-0.06 (-0.28-0.17)	0.93***
P8	Non-divers	0.78 (0.63-0.94)	-0.22 (-0.59-0.14)	0.93***
	Divers	0.71 (0.56-0.86)	-0.02 (-0.36-0.32)	0.94***

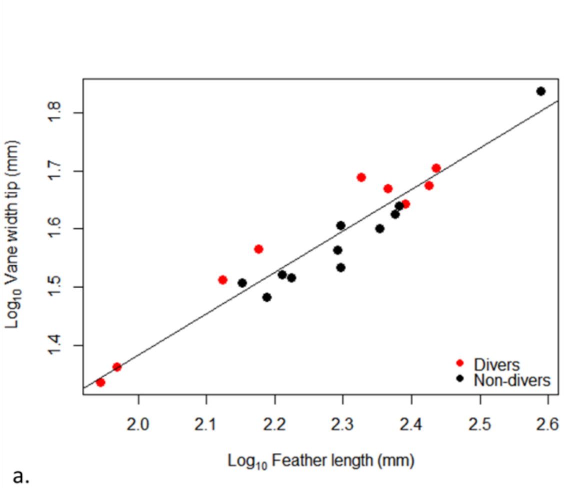
	Procellariidae	0.71 (0.60-0.82)	-0.04 (-0.28-0.21)	0.91***
P9	Non-divers	0.79 (0.64-0.94)	-0.26 (-0.61-0.10)	0.93***
	Divers	0.69 (0.60-0.80)	0.00 (-0.19-0.19)	0.98***
	Procellariidae	0.71 (0.63-0.79)	-0.05 (-0.23-0.13)	0.95***
P10	Non-divers	0.72 (0.53-0.91)	-0.07 (-0.50-0.36)	0.88***
	Divers	0.70 (0.60-0.80)	-0.02 (-0.25-0.21)	0.97***
	Procellariidae	0.70 (0.61-0.78)	-0.01 (-0.21-0.18)	0.94***

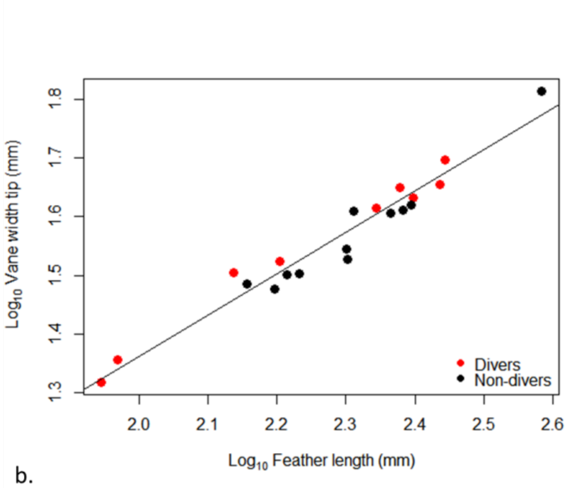
*P<0.05 **P<0.01 ***P<0.001

Appendix 5b: The allometric relationship between secondary feather length and vane width at the tip of the feather.

Feather	**Group**	**Slope (94% CI)**	**Intercept (95% CI)**	**R^2**
S1	Non-divers	0.79 (0.67-0.91)	0.05 (-0.19-0.29)	0.96***
	Divers	0.85 (0.77-0.93)	-0.05 (-0.21-0.10)	0.99***
	Procellariidae	0.81 (0.74-0.88)	0.01 (-0.13-0.14)	0.97***
S2	Non-divers	0.88 (0.69-1.06)	-0.12 (-0.48-0.25)	0.92***
	Divers	0.92 (0.79-1.06)	-0.20 (-0.46-0.06)	0.98***
	Procellariidae	0.90 (0.80-0.99)	-0.16 (-0.34-0.03)	0.96***
S3	Non-divers	0.85 (0.73-0.98)	-0.09 (-0.34-0.16)	0.96***
	Divers	0.79 (0.67-0.91)	0.06 (-0.17-0.29)	0.97***
	Procellariidae	0.79 (0.70-0.88)	0.05 (-0.13-0.23)	0.95***
S4	Non-divers	0.95 (0.78-1.13)	-0.28 (-0.62-0.06)	0.94***
	Divers	0.87 (0.80-0.94)	-0.12 (-0.26-0.01)	0.99***
	Procellariidae	0.91 (0.83-0.99)	-0.19 (-0.35- -0.04)	0.97***
S5	Non-divers	0.88 (0.69-1.06)	-0.13 (-0.49-0.23)	0.92***
	Divers	0.80 (0.68-0.92)	0.03 (-0.19-0.26)	0.98***
	Procellariidae	0.81 (0.72-0.91)	-0.01 (-0.20-0.17)	0.95***
S6	Non-divers	0.94 (0.81-1.07)	-0.26 (-0.52- -0.02)	0.96***
	Divers	0.86 (0.78-0.95)	-0.10 (-0.26-0.05)	0.99***
	Procellariidae	0.88 (0.81-0.95)	-0.14 (-0.28- -0.01)	0.97***
S7	Non-divers	0.99 (0.82-1.15)	-0.35 (-0.67- -0.03)	0.95***
	Divers	0.75 (0.67-0.83)	0.11 (-0.04-0.27)	0.99***
	Procellariidae	0.83 (0.74-0.92)	-0.04 (-0.22-0.14)	0.95***
S8	Non-divers	0.93 (0.78-1.08)	-0.26 (-0.55-0.04)	0.95***
	Divers	0.77 (0.60-0.95)	0.06 (-0.27-0.39)	0.94***
	Procellariidae	0.81 (0.71-0.92)	-0.03 (-0.23-0.17)	0.94***
S9	Non-divers	0.87 (0.66-1.09)	-0.15 (-0.58-0.28)	0.89***
	Divers	0.72 (0.59-0.85)	0.17 (-0.07-0.42)	0.96***
	Procellariidae	0.75 (0.64-0.86)	0.10 (-0.12-0.31)	0.92***
S10	Non-divers	0.85 (0.72-0.99)	-0.11 (-038-0.15)	0.95***
	Divers	0.75 (0.64-0.85)	0.11 (-0.08-0.31)	0.98***
	Procellariidae	0.76 (0.69-0.84)	0.07 (-0.08-0.21)	0.96***

*P<0.05 **P<0.01 ***P<0.001





Appendix 5c: The distal primary feathers a) P8 (slope: 071 (95% CI 0.60-0.80) and intercept: -0.04 (95% CI -0.28-0.21)) and b) P9 (slope: 0.71 (95% CI 0.63-0.79) and intercept: -0.05 (95% CI -0.23-0.13)) showing how vane width in the tip outer primaries of underwater divers are broader relative to feather length compared to petrels that do not dive underwater.

Appendix 6a: The slope comparison of primary vane width between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
	Vane width base			
Feather length	<0.0001	<0.0001	2,87	0,11
Group	<0.0001	<0.0001	0,58	0,46
Featherlength:Group	<0.0001	<0.0001	0,06	0,81
	Vane width middle			
Feather length	<0.0001	<0.0001	0	1
Group	<0.0001	<0.0001	0,15	0,71
Featherlength:Group	<0.0001	<0.0001	0,89	0,36
	Vane width tip			
Feather length	<0.0001	<0.0001	1,47	0,24
Group	<0.0001	<0.0001	0,38	0,55
Featherlength:Group	<0.0001	<0.0001	0,04	0,85

Appendix 6b: The slope comparison of secondary vane width between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
		Vane width base		
Feather length	<0.0001	<0.0001	1,95	0,18
Group	<0.0001	<0.0001	0,91	0,36
Featherlength:Group	<0.0001	<0.0001	0,2	0,66
		Vane width middle		
Feather length	<0.0001	<0.0001	1,91	0,19
Group	<0.0001	<0.0001	1,02	0,33
Featherlength:Group	<0.0001	<0.0001	0,37	0,55
		Vane width tip		
Feather length	<0.0001	<0.0001	0,64	0,44
Group	<0.0001	<0.0001	3,22	0,09
Featherlength:Group	<0.0001	<0.0001	0,13	0,72

Appendix 7a: The allometric relationship between primary feather length and barb length at the base of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.78 (0.64-0.92)	-0.07 (-0.37-0.22)	0.94***
	Divers	1.12 (0.87-1.37)	-0.72 (-1.21- -0.22)	0.93***
	Procellariidae	0.93 (0.77-1.09)	-0.36 (-0.68- -0.05)	0.89***
P2	Non-divers	0.80 (0.68-0.91)	-0.14 (-0.38-0.09)	0.96***
	Divers	1.09 (0.91-1.27)	0.71 (-1.09- -0.34)	0.96***
	Procellariidae	0.93 (0.81-1.06)	-0.41 (-0.66- -0.16)	0.93***
P3	Non-divers	0.83 (0.74-0.92)	-0.25 (-0.44- -0.06)	0.98***
	Divers	0.92 (0.72-1.13)	-0.42 (-0.85- -0.01)	0.93***
	Procellariidae	0.86 (0.76-0.97)	-0.31 (-0.53- -0.09)	0.94***
P4	Non-divers	0.90 (0.82-0.98)	-0.45 (-0.62- -0.28)	0.99***
	Divers	0.87 (0.71-1.02)	-0.35 (-0.68- -0.02)	0.95***
	Procellariidae	0.86 (0.77-0.95)	-0.35 (-0.54- -0.15)	0.95***
P5	Non-divers	0.90 (0.86-0.94)	-0.48 (-0.57- -0.38)	1.00***
	Divers	0.84 (0.73-0.97)	-0.35 (-0.61- -0.08)	0.97***
	Procellariidae	0.85 (0.78-0.92)	-0.36 (-0.52- -0.20)	0.97***
P6	Non-divers	0.98 (0.89-1.06)	-0.68 (-0.87- -0.48)	0.98***
	Divers	0.82 (0.70-0.94)	-0.30 (-0.57- -0.03)	0.97***
	Procellariidae	0.85 (0.77-0.94)	-0.39 (-0.58- -0.20)	0.96***
P7	Non-divers	1.02 (0.91-1.13)	-0.81 (-1.06- -0.56)	0.98***
	Divers	0.77 (0.62-0.92)	-0.20 (-0.52- -0.13)	0.95***
	Procellariidae	0.82 (0.70-0.93)	-0.33 (-0.59- -0.07)	0.92***

P8	Non-divers	0.93 (0.81-1.06)	-0.64 (-0.92- -0.36)	0.97***
	Divers	0.80 (0.67-0.93)	-0.29 (-0.58- -0.00)	0.96***
	Procellariidae	0.82 (0.72-0.91)	-0.36 (-0.58- -0.14)	0.94***
P9	Non-divers	0.93 (0.82-1.04)	-0.64 (-0.92- -0.36)	0.97***
	Divers	0.77 (0.66-0.89)	-0.26 (-0.52- 0.01)	0.97***
	Procellariidae	0.80 (0.71-0.80)	-0.34 (-0.54- -0.13)	0.95***
P10	Non-divers	0.88 (0.72-1.03)	-0.53 (-0.88- -0.18)	0.94***
	Divers	0.72 (0.61-0.82)	-0.13 (-0.36-0.11)	0.97***
	Procellariidae	0.74 (0.64-0.85)	-0.21 (-0.44-0.03)	0.92***

*P<0.05 **P<0.01 ***P<0.001

Appendix 7b: The allometric relationship between secondary feather length and barb length at the base of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.75 (0.62-0.89)	0.01 (-0.26-0.27)	0.94***
	Divers	1.00 (0.88-1.12)	-0.47 (-0.70- -0.24)	0.98***
	Procellariidae	0.89 (0.78-0.99)	-0.25 (-0.46- -0.05)	0.95***
S2	Non-divers	0.72 (0.52-0.92)	0.08 (-0.31-0.46)	0.87***
	Divers	0.93 (0.79-1.07)	-0.31 (-0.58- -0.05)	0.98***
	Procellariidae	0.83 (0.71-0.95)	-0.13 (-0.36-0.10)	0.93***
S3	Non-divers	0.55 (0.32-0.79)	0.41 (-0.05-0.87)	0.73***
	Divers	0.90 (0.74-1.07)	-0.24 (-0.56-0.07)	0.96***
	Procellariidae	0.74 (0.59-0.90)	0.04 (-0.26-0.35)	0.85***
S4	Non-divers	0.80 (0.50-1.10)	-0.07 (-0.65-0.52)	0.78***
	Divers	0.79 (0.66-0.91)	-0.01 (-0.25-0.23)	0.97***
	Procellariidae	0.77 (0.63-0.91)	0.01 (-0.27-0.28)	0.88***
S5	Non-divers	0.75 (0.46-1.04)	0.02 (-0.55-0.60)	0.76***
	Divers	0.78 (0.71-0.85)	-0.01 (-0.15-0.13)	0.99***
	Procellariidae	0.74 (0.60-0.88)	0.04 (-0.23-0.31)	0.87***
S6	Non-divers	0.80 (0.56-1.04)	-0.07 (-0.54-0.39)	0.85***
	Divers	0.70 (0.62-0.77)	0.16 (0.01-0.31)	0.99***
	Procellariidae	0.71 (0.59-0.83)	0.11 (-0.12-0.34)	0.90***
S7	Non-divers	0.72 (0.49-0.95)	0.09 (-0.37-0.55)	0.83***
	Divers	0.69 (0.61-0.77)	0.17 (0.02-0.32)	0.99***
	Procellariidae	0.68 (0.57-0.79)	0.18 (-0.04-0.39)	0.90***
S8	Non-divers	0.66 (0.39-0.93)	0.21 (-0.33-0.75)	0.74***
	Divers	0.67 (0.57-0.78)	0.22 (0.02-0.42)	0.97***
	Procellariidae	0.64 (0.51-0.77)	0.25 (0.00-0.51)	0.86***
S9	Non-divers	0.69 (0.43-0.96)	0.15 (-0.37-0.66)	0.78***
	Divers	0.72 (0.52-0.91)	0.11 (-0.25-0.48)	0.92***
	Procellariidae	0.70 (0.57-0.83)	0.14 (-0.11-0.39)	0.88***
S10	Non-divers	0.67 (0.50-0.84)	0.19 (-0.14-0.53)	0.88***
	Divers	0.81 (0.53-1.10)	-0.07 (-0.62-0.47)	0.87***
	Procellariidae	0.76 (0.62-0.90)	0.02 (-0.25-0.29)	0.88***

*P<0.05 **P<0.01 ***P<0.001

Appendix 8a: The allometric relationship between primary feather length and barb length at the middle of the feather.

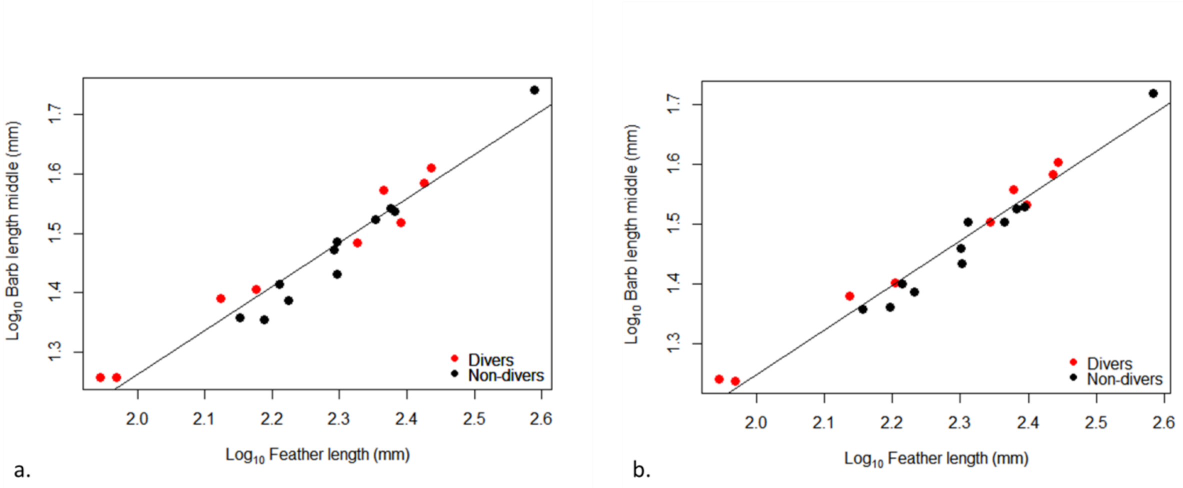
Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.75 (0.68-0.82)	-0.05 (-0.19-0.08)	0.98***
	Divers	1.00 (0.87-1.13)	-0.54 (-0.80- -0.28)	0.98***
	Procellariidae	0.87 (0.78-0.96)	-0.29 (-0.47- -0.11)	0.96***
P2	Non-divers	0.78 (0.61-0.95)	-0.16 (-0.51-0.19)	0.91***
	Divers	0.88 (0.72-1.05)	-0.35 (-0.69- -0.02)	0.95***
	Procellariidae	0.82 (0.71-0.93)	-0.24 (-0.46- -0.01)	0.93***
P3	Non-divers	0.78 (0.65-0.91)	-0.21 (-0.48- -0.07)	0.95***
	Divers	0.80 (0.64-0.95)	-0.21 (-0.55-0.12)	0.95***
	Procellariidae	0.77 (0.68-0.87)	-0.18 (-0.38-0.03)	0.94***
P4	Non-divers	0.82 (0.69-0.95)	-0.33 (-0.61- -0.05)	0.95***
	Divers	0.76 (0.61-0.90)	-0.16 (-0.47-0.15)	0.95***
	Procellariidae	0.77 (0.68-0.86)	-0.20 (-0.40- -0.00)	0.94***
P5	Non-divers	0.84 (0.75-0.93)	-0.39 (-0.58- -0.19)	0.98***
	Divers	0.74 (0.67-0.81)	-0.14 (-0.29-0.01)	0.99***
	Procellariidae	0.76 (0.68-0.83)	-0.19 (-0.36- -0.02)	0.96***
P6	Non-divers	0.88 (0.76-1.00)	-0.50 (-0.78- -0.23)	0.96***
	Divers	0.73 (0.65-0.81)	-0.13 (-0.30-0.04)	0.98***
	Procellariidae	0.76 (0.67-0.84)	-0.21 (-0.40- -0.02)	0.95***
P7	Non-divers	0.94 (0.81-1.07)	-0.66 (-0.96- -0.36)	0.96***
	Divers	0.70 (0.58-0.81)	-0.07 (-0.33-0.18)	0.96***
	Procellariidae	0.75 (0.65-0.85)	-0.21 (-0.44-0.03)	0.92***
P8	Non-divers	0.91 (0.79-1.02)	-0.61 (-0.88- -0.35)	0.97***
	Divers	0.69 (0.58-0.80)	-0.09 (-0.33-0.16)	0.97***
	Procellariidae	0.74 (0.65-0.83)	-0.22 (-0.43- -0.01)	0.94***
P9	Non-divers	0.86 (0.75-0.98)	-0.52 (-0.79- -0.25)	0.97***
	Divers	0.72 (0.65-0.78)	-0.16 (-0.31- -0.02)	0.99***
	Procellariidae	0.75 (0.67-0.82)	-0.24 (-0.41- -0.08)	0.96***
P10	Non-divers	0.86 (0.69-1.02)	-0.52 (-0.89- -0.15)	0.94***
	Divers	0.67 (0.59-0.76)	-0.06 (-0.25-0.13)	0.98***
	Procellariidae	0.71 (0.61-0.81)	-0.16 (-0.39-0.07)	0.92***

*P<0.05 **P<0.01 ***P<0.001

Appendix 8b: The allometric relationship between secondary feather length and barb length at the middle of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.72 (0.53-0.91)	0.09 (-0.29-0.69)	0.88***
	Divers	0.84 (0.77-0.92)	-0.15 (-0.29- -0.01)	0.99***
	Procellariidae	0.79 (0.70-0.88)	-0.05 (-0.23-0.13)	0.95***
S2	Non-divers	0.67 (0.43-0.92)	0.20 (-0.29-0.69)	0.79***
	Divers	0.80 (0.71-0.89)	-0.04 (-0.21-0.13)	0.99***
	Procellariidae	0.75 (0.64-0.86)	0.05 (-0.17-0.27)	0.91***
S3	Non-divers	0.61 (0.30-0.93)	0.32 (-0.30-0.95)	0.64**
	Divers	0.75 (0.65-0.85)	0.06 (-0.13-0.25)	0.98***
	Procellariidae	0.69 (0.55-0.84)	0.17 (-0.11-0.44)	0.86***
S4	Non-divers	0.69 (0.35-1.02)	0.19 (-0.47-0.85)	0.67**
	Divers	0.80 (0.74-0.85)	-0.02 (-0.12-0.08)	1.00***
	Procellariidae	0.75 (0.61-0.90)	0.06 (-0.21-0.33)	0.88***
S5	Non-divers	0.58 (0.24-0.91)	0.41 (-0.25-1.07)	0.58**
	Divers	0.80 (0.72-0.89)	-0.03 (-0.18-0.13)	0.99***
	Procellariidae	0.71 (0.55-0.86)	0.15 (-0.15-0.45)	0.84***
S6	Non-divers	0.58 (0.27-0.89)	0.40 (-0.21-1.02)	0.62**
	Divers	0.77 (0.68-0.87)	0.03 (-0.15-0.22)	0.98***
	Procellariidae	0.69 (0.55-0.84)	0.18 (-0.10-0.46)	0.85***
S7	Non-divers	0.56 (0.24-0.87)	0.45 (-0.17-1.07)	0.60**
	Divers	0.80 (0.71-0.88)	-0.01 (-0.18-0.15)	0.99***
	Procellariidae	0.71 (0.56-0.85)	0.16 (-0.12-0.43)	0.86***
S8	Non-divers	0.57 (0.27-0.87)	0.42 (-0.17-1.01)	0.64**
	Divers	0.82 (0.72-0.92)	-0.06 (-0.26-0.13)	0.98***
	Procellariidae	0.74 (0.60-0.87)	0.10 (-0.17-0.36)	0.88***
S9	Non-divers	0.57 (0.27-0.87)	0.43 (-0.17-1.02)	0.63**
	Divers	0.90 (0.64-1.15)	-0.22 (-0.70-0.27)	0.91***
	Procellariidae	0.80 (0.62-0.98)	-0.03 (-0.37-0.31)	0.84***
S10	Non-divers	0.52 (0.23-0.81)	0.53 (-0.04-1.11)	0.60**
	Divers	0.96 (0.64-1.27)	-0.33 (-0.94-0.27)	0.88***
	Procellariidae	0.84 (0.64-1.04)	-0.10 (-0.48-0.29)	0.81***

*P<0.05 **P<0.01 ***P<0.001



Appendix 8c: The distal primary feathers a) P8 (slope: 0.74 (95% CI 0.65-0.83) and intercept: -0.22 (95% CI -0.43- -0.01)) and b) P9 (slope: 0.75 (95% CI 0.67-0.82) and intercept: -0.24 (95% CI -0.41- -0.08)) showing how barb length in the middle outer primaries of underwater divers are longer compared to petrels that do not dive underwater.

Appendix 9a: The allometric relationship between primary feather length and barb length at the tip of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	0.68 (0.47-0.89)	-0.15 (-0.57-0.27)	0.84***
	Divers	0.75 (0.54-0.97)	-0.29 (-0.72-0.13)	0.90***
	Procellariidae	0.72 (0.59-0.85)	-0.23 (-0.48-0.03)	0.88***
P2	Non-divers	0.72 (0.47-0.96)	-0.28 (-0.78-0.23)	0.81***
	Divers	0.76 (0.56-0.96)	-0.34 (-0.75-0.06)	0.91***
	Procellariidae	0.73 (0.59-0.87)	-0.29 (-0.58- -0.00)	0.86***
P3	Non-divers	0.73 (0.48-0.97)	-0.31 (-0.82-0.20)	0.82***
	Divers	0.66 (0.50-0.82)	-0.16 (-0.50-0.17)	0.92***
	Procellariidae	0.68 (0.55-0.82)	-0.21 (-0.48-0.06)	0.87***
P4	Non-divers	0.72 (0.44-1.00)	-0.31 (-0.93-0.31)	0.76***
	Divers	0.65 (0.51-0.79)	-0.13 (-0.42-0.16)	0.94***
	Procellariidae	0.68 (0.52-0.80)	-0.21 (-0.47-0.13)	0.87***
P5	Non-divers	0.73 (0.54-0.92)	-0.32 (-0.75-0.10)	0.88***
	Divers	0.66 (0.53-0.80)	-0.16 (-0.45-0.14)	0.94***
	Procellariidae	0.68 (0.58-0.78)	-0.20 (-0.42-0.02)	0.91***
P6	Non-divers	0.81 (0.59-1.03)	-0.50 (-1.00-0.00)	0.87***
	Divers	0.70 (0.59-0.82)	-0.24 (-0.50-0.01)	0.96***
	Procellariidae	0.73 (0.63-0.84)	-0.31 (-0.54- -0.08)	0.92***
P7	Non-divers	0.80 (0.61-1.00)	-0.47 (-0.92- -0.02)	0.89***
	Divers	0.70 (0.60-0.81)	-0.24 (-0.48- -0.00)	0.87***
	Procellariidae	0.73 (0.64-0.82)	-0.30 (-0.50- -0.10)	0.94***
P8	Non-divers	0.80 (0.65-0.96)	-0.49 (-0.84- -0.13)	0.93***

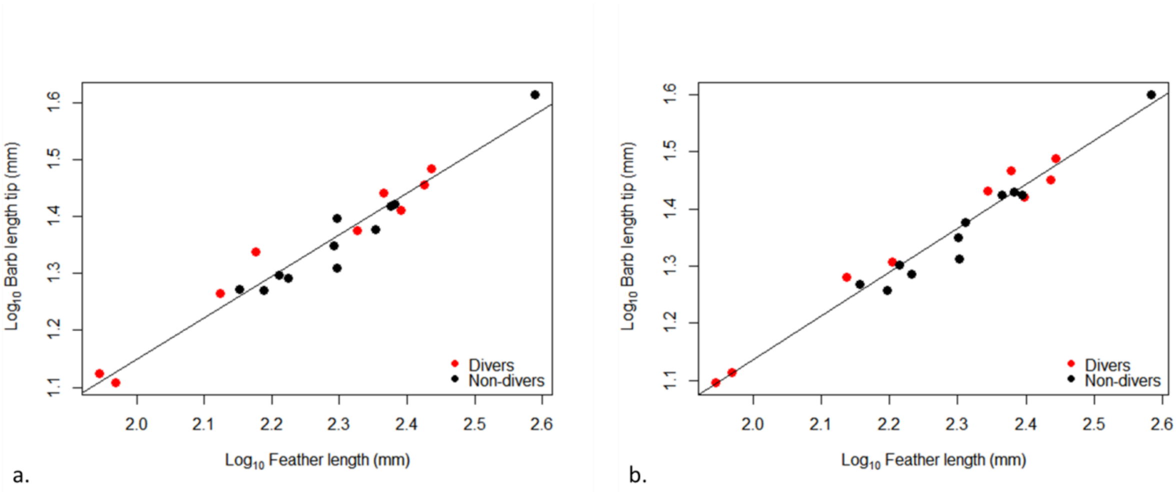
	Divers	0.71 (0.59-0.84)	-0.26 (-0.54- -0.02)	0.96***
	Procellariidae	0.73 (0.65-0.82)	-0.31 (-0.51- -0.12)	0.94***
P9	Non-divers	0.83 (0.69-0.96)	-0.54 (-0.85- -0.24)	0.95***
	Divers	0.76 (0.66-0.86)	-0.37 (-0.60- -0.14)	0.97***
	Procellariidae	0.77 (0.69-0.84)	-0.39 (-0.57- -0.22)	0.96***
P10	Non-divers	0.84 (0.71-0.97)	-0.58 (-0.88- -0.29)	0.95***
	Divers	0.79 (0.66-0.90)	-0.41 (-0.68- -0.15)	0.97***
	Procellariidae	0.78 (0.69-0.87)	-0.43 (-0.63- -0.24)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Appendix 9b: The allometric relationship between secondary feather length and barb length at the tip of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.64 (0.50-0.79)	0.07 (-0.23-0.36)	0.90***
	Divers	0.72 (0.60-0.85)	-0.09 (-0.33-0.85)	0.97***
	Procellariidae	0.70 (0.61-0.78)	-0.03 (-0.20-0.13)	0.94***
S2	Non-divers	0.71 (0.51-0.91)	-0.04 (-0.43-0.36)	0.87***
	Divers	0.86 (0.76-0.97)	-0.35 (-0.55- -0.16)	0.98***
	Procellariidae	0.82 (0.71-0.92)	-0.25 (-0.46- -0.05)	0.96***
S3	Non-divers	0.72 (0.49-0.96)	-0.05 (-0.51-0.41)	0.83***
	Divers	0.69 (0.51-0.87)	0.00 (-0.34-0.35)	0.93***
	Procellariidae	0.70 (0.58-0.82)	-0.01 (-0.25-0.22)	0.90***
S4	Non-divers	0.85 (0.74-0.95)	-0.28 (-0.50- -0.07)	0.97***
	Divers	0.82 (0.69-0.96)	-0.26 (-0.52-0.00)	0.97***
	Procellariidae	0.85 (0.77-0.93)	-0.3 (-0.46- -0.14)	0.96***
S5	Non-divers	0.73 (0.59-0.87)	-0.04 (-0.32-0.23)	0.93***
	Divers	0.82 (0.71-0.94)	-0.25 (-0.48- -0.03)	0.98***
	Procellariidae	0.80 (0.71-0.89)	-0.20 (-0.36 -0.03)	0.96***
S6	Non-divers	0.72 (0.39-1.05)	-0.03 (-0.68-0.62)	0.70***
	Divers	0.85 (0.77-0.94)	-0.30 (-0.47- -0.13)	0.99***
	Procellariidae	0.80 (0.67-0.96)	-0.20 (-0.50-0.06)	0.96***
S7	Non-divers	0.84 (0.72-0.95)	-0.27 (-0.49- -0.05)	0.97***
	Divers	0.88 (0.79-0.98)	-0.37 (-0.56- -0.05)	0.99***
	Procellariidae	0.88 (0.81-0.94)	-0.35 (-0.48- -0.23)	0.98***
S8	Non-divers	0.78 (0.65-0.91)	-0.16 (-0.42-0.10)	0.95***
	Divers	0.82 (0.68-0.95)	-0.24 (-0.50-0.02)	0.97***
	Procellariidae	0.81 (0.73-0.88)	-0.22 (-0.37- -0.07)	0.97***
S9	Non-divers	0.79 (0.64-0.95)	-0.19 (-0.50-0.12)	0.93***
	Divers	0.86 (0.68-1.04)	-0.33 (-0.67-0.01)	0.93***
	Procellariidae	0.85 (0.75-0.94)	-0.30 (-0.48- -0.11)	0.95***
S10	Non-divers	0.81 (0.66-0.97)	-0.24 (-0.53-0.06)	0.94***
	Divers	0.95 (0.53-1.38)	-0.51 (-1.32-0.30)	0.81***
	Procellariidae	0.91 (0.72-1.10)	-0.43 (-0.80- -0.07)	0.85***

*P<0.05 **P<0.01 ***P<0.001



Appendix 9c: The distal primary feathers a) P8 (slope: 0.73 (95% CI 0.65-0.82) and intercept: -0.31 (95% CI -0.51- -0.12)) and b) P9 (slope: 0.77 (95% CI 0.69-0.84) and intercept: -0.39 (95% CI -0.57- -0.22)) showing how different the barb length in the tip of outer primaries of underwater divers are compared to petrels that do not dive underwater.

Appendix 10a: The slope comparison of primary barb length between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
	Barb length base			
Feather length	<0.0001	<0.0001	1,22	0,29
Group	<0.0001	<0.0001	5,94	0,03
Featherlength:Group	<0.0001	<0.0001	1,76	0,2
	Barb length middle			
Feather length	<0.0001	<0.0001	4,18	0,06
Group	<0.0001	<0.0001	1,59	0,23
Featherlength:Group	<0.0001	<0.0001	0,01	0,91
	Barb length tip			
Feather length	<0.0001	<0.0001	4,23	0,06
Group	<0.0001	<0.0001	1,68	0,21
Featherlength:Group	<0.0001	<0.0001	0,02	0,88

Appendix 10b: The slope comparison of secondary barb length between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
		Barb length base		
Feather length	<0.0001	<0.0001	0,04	0,85
Group	<0.0001	<0.0001	0,18	0,68
Featherlength:Group	<0.0001	<0.0001	0,24	0,63
		Barb length middle		
Feather length	<0.0001	<0.0001	0	0,98
Group	<0.0001	<0.0001	0,73	0,41
Featherlength:Group	<0.0001	<0.0001	0,57	0,46
		Barb length tip		
Feather length	<0.0001	<0.0001	0,04	0,85
Group	<0.0001	<0.0001	0,26	0,62
Featherlength:Group	<0.0001	<0.0001	0,27	0,61

Appendix 11: The barbule density at the base for the 20 Procellariidae.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	-0.21 (-0.54-0.11)	1.78 (1.12-2.43)	0.24
	Divers	0.06 (-0.16-0.28)	1.22 (0.78-1.67)	-0.09
	Procellariidae	0.02 (-0.12-0.17)	1.30 (1.01-1.59)	-0.07
P4	Non-divers	-0.18 (-0.61-0.25)	1.71 (0.81-2.62)	0.02
	Divers	0.09 (-0.20-0.39)	1.17 (0.54-1.79)	-0.06
	Procellariidae	0.05 (-0.14-0.25)	1.24 (0.84-1.65)	-0.05
P6	Non-divers	-0.13 (-0.35-0.10)	1.62 (1.13-2.11)	0.16
	Divers	0.21 (-0.04-0.46)	0.90 (0.35-1.44)	0.37
	Procellariidae	0.16 (0.01-0.32)	1.00 (0.65-1.35)	0.23
P8	Non-divers	-0.11 (-0.41-0.18)	1.60 (0.94-2.27)	0.00
	Divers	0.09 (-0.06-0.24)	1.15 (0.81-1.48)	0.19
	Procellariidae	0.06 (-0.04-0.17)	1.21 (0.97-1.44)	0.05
P10	Non-divers	0.07 (-0.27-0.40)	1.20 (0.44-1.96)	-0.14
	Divers	0.05 (-0.08-0.18)	1.24 (0.95-1.54)	-0.02
	Procellariidae	0.05 (-0.04-0.15)	1.24 (1.02-1.45)	0.02

*P<0.05 **P<0.01 ***P<0.001

Appendix 12: The slope comparison of primary barbule density between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
	Barbule density base			
Feather length	<0.0001	<0.0001	1,23	0,29
Group	<0.0001	<0.0001	0,32	0,57
Featherlength:Group	<0.0001	<0.0001	1,19	0,3
	Barbule density middle			
Feather length	<0.0001	<0.0001	0,03	0,87
Group	<0.0001	<0.0001	0,36	0,56
Featherlength:Group	<0.0001	<0.0001	0,18	0,68
	Barbule density tip			
Feather length	<0.0001	<0.0001	0,48	0,51
Group	<0.0001	<0.0001	3,1	0,11
Featherlength:Group	<0.0001	<0.0001	0,39	0,55

Appendix 13: Rachis and calamus depths of 20 Procellariids relative to feather length.

Section	Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
Tip	Primaries	Non-divers	0.93 (0.18-1.68)	-1.94 (-4.34-0.47)	0.41***
		Divers	1.00 (0.46-1.54)	-2.11 (-3.81- -0.40)	0.69**
		Procellariidae	0.95 (0.57-1.33)	-1.96 (-3.17--0.75)	0.58***
	Secondaries	Non-divers	1.35 (0.59-2.11)	-3.45 (-5.92- -0.99)	0.60***
		Divers	0.96 (0.83-1.20)	-2.22 (-2.65- -1.80)	0.98***
		Procellariidae	1.10 (0.79-1.42)	-2.66 (-3.67- -1.64)	0.75***
Middle	Primaries	Non-divers	0.72 (0.35-1.09)	-1.09 (-2.27- -0.10)	0.65***
		Divers	0.31 (0.01-0.60)	0.27 (-0.65-1.20)	0.39**
		Procellariidae	0.43 (0.20-0.65)	-0.12 (-0.85-0.61)	0.43***
	Secondaries	Non-divers	0.91 (0.59-1.23)	-1.67 (-2.71- -0.63)	0.80***
		Divers	1.15 (0.72-1.57)	-2.42 (-3.77- -1.07)	0.86***
		Procellariidae	1.06 (0.84-1.28)	-2.16 (-2.87- -1.44)	0.85***
Base	Primaries	Non-divers	1.14 (0.81-1.47)	-2.35 (-3.41- -1.29)	0.89***
		Divers	0.87 (0.60-0.12)	-1.43 (-2.26- -0.59)	0.88***
		Procellariidae	0.94 (0.75-1.14)	-1.69 (-2.30- -1.08)	0.85***
	Secondaries	Non-divers	0.82 (0.48-1.15)	-1.18 (-2.27- -0.08)	0.80***
		Divers	0.78 (0.70-0.85)	-1.04 (-1.29- -0.80)	0.99***
		Procellariidae	0.79 (0.66-0.93)	-1.09 (-1.53- -0.66)	0.89**
			Calamus width		
	Primaries	Non-divers	0.78 (0.70-0.86)	-1.03 (-1.28- -0.78)	0.98***

	Divers	1.05 (0.83-1.27)	-1.92 (-2.61- -1.22)	0.94***
	Procellariidae	0.96 (0.84-1.08)	-1.62 (-2.01- -1.24)	0.94***
Secondaries	Non-divers	1.11 (0.80-1.41)	-2.01 (-3.00- -1.01)	0.87***
	Divers	0.81 (0.48-1.13)	-1.02 (-2.04- -0.01)	0.84***
	Procellariidae	0.91 (0.72-1.10)	-1.34 (-1.96- -0.72)	0.84***

*P<0.05 **P<0.01 ***P<0.001

Appendix 14a: The slope comparison of primary calamus and rachis depths between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
	Calamus width			
Feather length	4795513	4795513	0,12	0,73
Group	24999686	24999686	0,625	0,44
Featherlength:Group	6061593	6061593	0,152	0,70
	Rachis depth base			
Feather length	<0.0001	<0.0001	0,249	0,63
Group	<0.0001	<0.0001	0,47	0,14
Featherlength:Group	<0.0001	<0.0001	0,005	0,95
	Rachis depth middle			
Feather length	<0.0001	<0.0001	4,375	0,05
Group	<0.0001	<0.0001	0,234	0,64
Featherlength:Group	<0.0001	<0.0001	0,275	0,61
	Rachis depth tip			
Feather length	<0.0001	<0.0001	3,68	0,07
Group	<0.0001	<0.0001	0,17	0,69
Featherlength:Group	<0.0001	<0.0001	0,07	0,79

Appendix 14b: The slope comparison of secondary calamus and rachis depths between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
		Calamus width		
Feather length	<0.0001	<0.0001	32,69	0
Group	<0.0001	<0.0001	2,28	0,15
Featherlength:Group	<0.0001	<0.0001	19,78	0

		Rachis depth base		
Feather length	<0.0001	<0.0001	4,12	0,05
Group	<0.0001	<0.0001	0,37	0,55
Featherlength:Group	<0.0001	<0.0001	9,55	0,01
		Rachis depth middle		
Feather length	<0.0001	<0.0001	2,29	0,15
Group	<0.0001	<0.0001	1,26	0,28
Featherlength:Group	<0.0001	<0.0001	2,56	0,13
		Rachis depth tip		
Feather length	<0.0001	<0.0001	0,13	0,73
Group	<0.0001	<0.0001	0,24	0,63
Featherlength:Group	<0.0001	<0.0001	0,21	0,66

Appendix 15a: Rachis depth relative to feather length in the middle of the primary feathers.

Feather	**Group**	**Slope (95% CI)**	**Intercept (95% CI)**	R^2
P1	Non-divers	0.62 (-0.27-1.51)	-1.09 (-2.89-0.72)	0.13
	Divers	-0.16 (-0.77-0.45)	0.46 (-0.74-1.67)	-0.08
	Procellariidae	0.19 (-0.31-0.68)	-0.22 (-1.21-0.78)	-0.20
P2	Non-divers	0.40 (-0.17-0.98)	-0.66 (-1.84-0.52)	0.13
	Divers	-0.41 (-0.81--0.01)	1.00 (0.18-1.81)	0.38*
	Procellariidae	-0.01 (-0.37-0.36)	0.18 (-0.57-0.93)	-0.06
P3	Non-divers	0.51 (-0.17-1.20)	-0.89 (-2.34-0.56)	0.16
	Divers	-0.23 (-0.64-0.17)	0.62 (-0.22-1.46)	0.09
	Procellariidae	0.12 (-0.27-0.51)	-0.08 (-0.89-0.73)	-0.03
P4	Non-divers	0.34 (-0.38-1.05)	-0.52 (-2.08-1.04)	0.01
	Divers	0.04 (-0.54-0.62)	0.10 (-1.13-1.33)	-0.14
	Procellariidae	0.20 (-0.18-0.59)	-0.24 (-1.06-0.59)	0.01
P5	Non-divers	0.63 (0.01-1.24)	-1.19 (-2.56-0.17)	0.30
	Divers	0.28 (-0.29-0.86)	-0.37 (-1.62-0.88)	0.04
	Procellariidae	0.34 (0.03-0.74)	-0.62 (-1.41-0.16)	0.18*
P6	Non-divers	0.76 (0.12-1.41)	-1.49 (-2.96- -0.02)	0.38*
	Divers	0.43 (-0.09-0.94)	-0.66 (-1.79-0.47)	0.26
	Procellariidae	0.52 (0.16-0.87)	-0.89 (-1.70- -0.09)	0.30**
P7	Non-divers	0.97 (0.38-1.56)	-1.98 (-3.33- -0.63)	0.56**
	Divers	0.56 (0.10-1.01)	-0.95 (-1.97-0.06)	0.48*
	Procellariidae	0.65 (0.31-0.99)	-1.21 (-1.98- -0.44)	0.45***
P8	Non-divers	1.14 (0.46-1.81)	-2.39 (-3.95- -0.83)	0.58**
	Divers	0.56 (0.11-1.01)	-0.94 (-1.94-0.06)	0.49*
	Procellariidae	0.67 (0.28-1.06)	-1.25 (-2.14- -0.37)	0.39**
P9	Non-divers	1.18 (0.55-1.81)	-2.46 (-3.91- -0.99)	0.63**
	Divers	0.52 (0.05-1.09)	-0.86 (-2.15-0.42)	0.32
	Procellariidae	0.68 (0.28-1.08)	-1.27 (-2.19- -0.35)	0.38**
P10	Non-divers	1.02 (0.48-1.57)	-2.08 (-3.34- -0.82)	0.63**
	Divers	0.41 (-0.04-0.87)	-0.67 (-1.69-0.34)	0.36
	Procellariidae	0.64 (0.33-0.96)	-1.19 (-1.91- -0.46)	0.47***

*P<0.05 **P<0.01 ***P<0.001

Appendix 15b: Rachis depth relative to feather length in the middle of secondary feathers.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	0.39 (-0.38-1.15)	-0.53 (-2.04-0.99)	0.03
	Divers	-0.22 (-0.61-0.17)	0.56 (-0.19-1.32)	0.11
	Procellariidae	0.10 (-0.34-0.53)	0.00 (-0.85-0.85)	-0.04
S2	Non-divers	0.63 (-0.12-1.37)	-1.00 (-2.47-0.46)	0.21
	Divers	0.62 (-0.21-1.44)	-1.15 (-2.73-0.44)	0.25*
	Procellariidae	0.74 (0.20-1.29)	-1.30 (-2.37- -0.23)	0.29
S3	Non-divers	0.53 (-0.14-1.20)	-0.92 (-2.34-0.50)	0.18
	Divers	-0.23 (-0.67-0.21)	0.62 (-0.29-1.53)	0.06
	Procellariidae	0.16 (-0.23-0.55)	-0.16 (-0.98-0.65)	-0.01
S4	Non-divers	0.76 (-0.30-1.81)	-1.36 (-3.42-0.71)	0.14
	Divers	1.30 (0.21-2.38)	-2.42 (-4.50- -0.34)	0.52*
	Procellariidae	1.10 (0.48-1.73)	-2.05 (-3.25- -0.84)	0.42**
S5	Non-divers	0.69 (-0.25-1.63)	-1.26 (-3.10-0.58)	0.15
	Divers	1.92 (1.09-2.75)	-3.64 (-5.23- -2.05)	0.82**
	Procellariidae	1.44 (0.85-2.03)	-2.73 (-3.87- -1.58)	0.59***
S6	Non-divers	0.81 (0.13-1.49)	-1.59 (-3.13- -0.05)	0.38*
	Divers	0.45 (-0.07-0.96)	-0.70 (-1.84-0.43)	0.28
	Procellariidae	0.52 (0.16-0.87)	-0.89 (-1.70- -0.09)	0.30**
S7	Non-divers	0.91 (-0.24-2.04)	-1.73 (-3.97-0.52)	0.18
	Divers	2.01 (1.09-2.94)	-3.84 (-5.62- -2.06)	0.80**
	Procellariidae	1.59 (0.94-2.24)	-3.05 (-4.32- -1.78)	0.59***
S8	Non-divers	1.13 (0.48-1.79)	-2.37 (-3.88- -0.86)	0.59**
	Divers	0.58 (0.13-1.04)	-0.99 (-2.01-0.03)	0.51*
	Procellariidae	0.67 (0.28-1.06)	-1.25 (-2.14- -0.37)	0.39**
S9	Non-divers	1.12 (0.18-2.05)	-2.23 (-4.07- -0.39)	0.38*
	Divers	1.82 (1.00-2.64)	-3.48 (-5.06- -1.91)	0.80**
	Procellariidae	1.50 (0.93-2.07)	-2.94 (-4.04- -1.83)	0.63***
S10	Non-divers	1.62 (0.49-2.75)	-3.27 (-5.50- -1.05)	0.49*
	Divers	1.78 (0.90-2.67)	-3.41 (-5.10- -1.73)	0.77**
	Procellariidae	1.59 (0.95-2.23)	-3.14 (-4.38- -1.89)	0.59***

*P<0.05 **P<0.01 ***P<0.001

Appendix 16a: Rachis depth relative to feather length at the tip of primary feathers.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	1.26 (0.05-2.48)	-2.65 (-5.10- -0.20)	0.31*
	Divers	1.40 (0.65-1.15)	-2.73 (-4.21- -1.24)	0.70**
	Procellariidae	1.33 (0.59-2.06)	-2.70 (-4.18- -1.22)	0.41**
P2	Non-divers	1.06 (-0.13-2.25)	-2.25 (-4.69-0.19)	0.24
	Divers	1.58 (0.67-2.49)	-3.18 (-5.03- -1.34)	0.67**
	Procellariidae	1.25 (0.54-1.96)	-2.59 (-4.04- -1.14)	0.40**
P3	Non-divers	1.13 (-0.01-2.26)	-2.45 (-4.86- -0.03)	0.29
	Divers	1.62 (1.01-2.23)	-3.29 (-4.56- -2.02)	0.83***
	Procellariidae	1.32 (0.65-1.99)	-2.78 (-4.18- -1.38)	0.46***
P4	Non-divers	1.03 (-0.07-2.26)	-2.21 (-4.61-0.19)	0.26
	Divers	1.42 (0.76-2.08)	-2.95 (-4.34- -1.55)	0.76**
	Procellariidae	1.21 (0.65-1.78)	-2.56 (-3.77- -1.35)	0.51***
P5	Non-divers	0.89 (-0.18-1.95)	-1.95 (-4.31-0.42)	0.20
	Divers	1.11 (0.54-1.67)	-2.31 (-3.54- -1.08)	0.72**
	Procellariidae	0.96 (0.43-1.49)	-2.06 (-3.23- -0.90)	0.42**
P6	Non-divers	0.88 (-0.23-1.99)	-1.93 (-4.45-0.59)	0.18
	Divers	0.92 (0.26-1.58)	-1.96 (-3.42- -0.50)	0.55*
	Procellariidae	0.90 (0.35-1.44)	-1.94 (-3.15- -0.73)	0.37**
P7	Non-divers	0.81 (-0.16-1.99)	-1.80 (-4.04-0.44)	0.20
	Divers	0.72 (0.09-1.36)	-1.59 (-3.00- -0.19)	0.44*
	Procellariidae	0.79 (0.32-1.26)	-1.74 (-2.79- -0.68)	0.38**
P8	Non-divers	0.64 (-0.37-1.65)	-1.41 (-3.75-0.93)	0.10
	Divers	0.68 (0.02-1.36)	-1.50 (-3.03-0.03)	0.37
	Procellariidae	0.68 (0.20-1.16)	-1.49 (-2.54- -0.43)	0.29**
P9	Non-divers	0.87 (-0.10-1.85)	-1.88 (-4.13-0.38)	0.24
	Divers	0.50 (-0.08-1.09)	-1.11 (-2.42-0.21)	0.28
	Procellariidae	0.69 (0.23-1.15)	-1.49 (-2.54- -0.43)	0.32**
P10	Non-divers	1.04 (0.26-1.82)	-2.22 (-4.02- -0.43)	0.45**
	Divers	0.46 (-0.11-1.04)	-1.01 (-2.30-0.28)	0.25
	Procellariidae	0.71 (0.27-1.16)	-1.52 (-2.53-0.51)	0.36**

*P<0.05 **P<0.01 ***P<0.001

Appendix 16b: Rachis depth relative to feather length at the tip of secondary feathers.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	1.79 (0.61-2.96)	-3.65 (-5.98- -1.33)	0.52**
	Divers	1.42 (0.55-2.30)	-2.93 (-4.63- -1.23)	0.68**
	Procellariidae	1.56 (0.95-2.18)	-3.20 (-4.41- -2.00)	0.61***
S2	Non-divers	2.14 (0.49-3.80)	-4.41 (-7.68- -1.15)	0.43*
	Divers	1.54 (0.77-2.31)	-3.17 (-4.64- -1.69)	0.77**
	Procellariidae	1.72 (0.94-2.51)	-3.56 (-5.08- -2.03)	0.53***
S3	Non-divers	1.92 (0.20-3.63)	-4.00 (-7.38- -0.62)	0.35*
	Divers	1.07 (0.23-1.92)	-2.35 (-3.96- -0.73)	0.56*
	Procellariidae	1.38 (0.57-2.18)	-2.93 (-4.50- -1.37)	0.49**
S4	Non-divers	1.46 (0.06-2.86)	-3.18 (-5.92- -0.43)	0.31*
	Divers	0.87 (0.40-1.33)	-2.00 (-2.90- -1.11)	0.74**
	Procellariidae	1.08 (0.46-1.69)	-2.41 (-3.62- -1.21)	0.41**
S5	Non-divers	1.93 (0.60-3.26)	-4.08 (-6.69- -1.47)	0.49**
	Divers	0.71 (0.10-1.33)	-1.77 (-2.95- -0.59)	0.50*
	Procellariidae	1.22 (0.54-1.90)	-2.72 (-4.04- -1.40)	0.43**
S6	Non-divers	1.59 (0.18-3.00)	-3.47 (-6.24- -0.70)	0.36*
	Divers	0.72 (0.26-1.18)	-1.78 (-2.66- -0.89)	0.66**
	Procellariidae	1.05 (0.41-1.69)	-2.40 (-3.64- -1.16)	0.38**
S7	Non-divers	1.61 (0.07-3.16)	-3.52 (-6.56- -0.49)	0.31*
	Divers	0.41 (0.03-0.79)	-1.23 (-1.97- -0.50)	0.46*
	Procellariidae	0.88 (0.18-1.58)	-2.10 (-3.46- -0.73)	0.25*
S8	Non-divers	1.85 (0.33-3.36)	-4.00 (-6.96- -1.03)	0.40*
	Divers	0.60 (0.04-1.16)	-1.57 (-2.65- -0.50)	0.45*
	Procellariidae	1.02 (0.33-1.71)	-2.38 (-3.72- -1.03)	0.33**
S9	Non-divers	1.76 (0.11-3.41)	-3.83 (-7.08- -0.60)	0.32*
	Divers	0.69 (0.43-0.96)	-1.79 (-2.29- -1.28)	0.85***
	Procellariidae	1.05 (0.37-1.72)	-2.45 (-3.76- -1.14)	0.35**
S10	Non-divers	1.84 (0.27-3.40)	-4.00 (-7.07- -0.92)	0.38*
	Divers	0.54 (0.09-0.98)	-1.49 (-2.34- -0.64)	0.53*
	Procellariidae	0.93 (0.27-1.59)	-2.23 (-3.52- -0.95)	0.30**

*P<0.05 **P<0.01 ***P<0.001

Appendix 17a: The allometric relationship between primary feather length and rachis depth at the base of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P1	Non-divers	1.22 (0.65-1.78)	-2.20 (-3.34- -1.06)	0.69***
	Divers	0.64 (0.07-1.21)	-0.97 (-2.09-0.16)	0.43**
	Procellariidae	0.85 (0.45-1.24)	-1.42 (-2.21- -0.62)	0.50***
P2	Non-divers	1.17 (0.54-1.80)	-2.13 (-3.43- -0.83)	0.62***
	Divers	0.82 (0.27-1.37)	-1.40 (-2.51- -0.29)	0.59**
	Procellariidae	0.98 (0.61-1.36)	-1.74 (-2.50- -0.98)	0.61***
P3	Non-divers	1.10 (0.53-1.68)	-2.04 (-3.27- -0.63)	0.64**
	Divers	0.70 (0.21-1.18)	-1.15 (-2.15- -0.15)	0.57**
	Procellariidae	0.84 (0.50-1.75)	-1.47 (-2.17- -0.76)	0.58***
P4	Non-divers	1.11 (0.48-1.73)	-2.09 (-3.45- -0.73)	0.60**
	Divers	0.75 (0.42-1.08)	-1.33 (-2.03- -0.63)	0.78**
	Procellariidae	0.91 (0.60-1.21)	-1.66 (-2.31- -1.00)	0.67***
P5	Non-divers	1.18 (0.65-1.70)	-2.29 (-3.45- -1.12)	0.71***
	Divers	0.82 (0.49-1.15)	-1.49 (-2.21- -0.78)	0.81***
	Procellariidae	0.94 (0.68-1.21)	-1.77 (-2.35- -1.19)	0.75***
P6	Non-divers	1.11 (0.60-1.62)	-2.19 (-3.34- -1.04)	0.70***
	Divers	0.89 (0.50-1.29)	-1.65 (-2.52- -0.79)	0.78***
	Procellariidae	0.94 (0.67-1.21)	-1.78 (-2.39- -1.16)	0.73***
P7	Non-divers	1.28 (0.88-1.68)	-2.58 (-3.51- -1.66)	0.84***
	Divers	1.00 (0.69-1.30)	-1.92 (-2.60- -1.24)	0.88***
	Procellariidae	1.07 (0.85-1.28)	2.09 (-2.57- -1.60)	0.85***
P8	Non-divers	1.28 (1.02-1.54)	-2.65 (-3.25- -2.05)	0.93***
	Divers	0.91 (0.59-1.22)	-1.72 (-2.43- -1.00)	0.85***
	Procellariidae	0.98 (0.76-1.19)	-1.91 (-2.40- -1.42)	0.83***
P9	Non-divers	1.34 (0.93-1.77)	-2.77 (-3.74- -1.79)	0.84***
	Divers	0.98 (0.67-1.28)	-1.85 (-2.54- -1.17)	0.88***
	Procellariidae	1.05 (0.81-1.29)	-2.05 (-2.59- -1.51)	0.82***
P10	Non-divers	1.03 (0.61-1.45)	-1.95 (-2.92- -0.99)	0.75***
	Divers	0.85 (0.35-1.34)	-1.51 (-2.62- -0.41)	0.66**
	Procellariidae	0.88 (0.61-1.16)	-1.61 (-2.24- -0.98)	0.70***

*P<0.05 **P<0.01 ***P<0.001

Appendix 17b: The allometric relationship between secondary feather length and rachis depth at the base of the feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
S1	Non-divers	1.22 (0.71-1.73)	-2.18 (-3.19- -1.17)	0.74***
	Divers	0.63 (-0.20-1.46)	-0.91 (-2.53-0.70)	0.26
	Procellariidae	0.80 (0.34-1.26)	-1.30 (-2.21- -0.40)	0.41**
S2	Non-divers	0.93 (0.15-1.72)	-1.64 (-3.19- -0.08)	0.38*
	Divers	0.69 (-0.01-1.38)	-0.99 (-2.32-0.33)	0.41
	Procellariidae	0.66 (0.12-1.19)	-1.03 (-2.08-0.02)	0.24*
S3	Non-divers	1.15 (0.34-1.95)	-2.03 (-3.62- -0.44)	0.48*
	Divers	0.62 (-0.02-1.25)	-0.87 (-2.09-0.35)	0.40
	Procellariidae	0.71 (0.21-1.21)	-1.12 (-2.10- -0.14)	0.30**
S4	Non-divers	1.09 (0.47-1.71)	-1.94 (-3.16- -0.71)	0.59*
	Divers	0.56 (0.01-1.11)	-0.76 (-1.82-0.30)	0.42
	Procellariidae	0.64 (0.18-1.10)	-1.00 (-1.90- -0.11)	0.30**
S5	Non-divers	0.91 (-0.03-1.85)	-1.58 (-3.42-0.27)	0.28
	Divers	0.77 (0.09-1.46)	-1.23 (-2.54-0.09)	0.49*
	Procellariidae	0.77 (0.27-1.27)	-1.26 (-2.23- -0.29)	0.34**
S6	Non-divers	0.83 (-0.09-1.76)	-1.43 (-3.24-0.39)	0.24
	Divers	1.02 (0.35-1.68)	-1.75 (-3.03- -0.47)	0.65*
	Procellariidae	0.92 (0.45-1.39)	-1.59 (-2.50- -0.67)	0.47***
S7	Non-divers	0.69 (-0.28-1.67)	-1.17 (-3.08-0.74)	0.14
	Divers	0.76 (0.21-1.32)	-1.27 (-2.33- -0.20)	0.60*
	Procellariidae	0.71 (0.25-1.16)	-1.18 (-2.06- -0.30)	0.35**
S8	Non-divers	0.69 (-0.28-1.59)	-1.16 (-2.93-0.60)	0.17
	Divers	0.66 (0.12-1.21)	-1.09 (-2.14- -0.04)	0.53*
	Procellariidae	0.65 (0.24-1.07)	-1.09 (-1.89- -0.28)	0.36**
S9	Non-divers	0.68 (-0.26-1.62)	-1.16 (-2.93-0.60)	0.14
	Divers	0.84 (0.23-1.45)	-1.50 (-2.67- -0.33)	0.59*
	Procellariidae	0.82 (0.38-1.26)	-1.44 (-2.30- -0.58)	0.44**
S10	Non-divers	0.76 (-0.23-1.74)	-1.31 (-3.25-0.62)	0.17
	Divers	0.80 (0.17-1.43)	-1.44 (-2.65- -0.23)	0.55*
	Procellariidae	0.82 (0.37-1.27)	-1.46 (-2.33- -0.59)	0.44**

*P<0.05 **P<0.01 ***P<0.001

Appendix 18a: The allometric relationship between feather length and rachis stiffness at 4 degrees at the base of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.85 (1.21-2.49)	-4.10 (-5.41- -2.79)	0.81***
	Divers	2.23 (0.50-3.97)	-5.02 (-8.53- -1.52)	0.51*
	Procellariidae	2.12 (1.32-2.92)	-4.72 (-6.35- -3.09)	0.61***
	Procellariiformes	2.54 (2.03-3.05)	-5.54 (-6.61- -4.49)	0.79***
P4	Non-divers	1.53 (0.97-2.09)	-3.64 (-4.86- -2.42)	0.79***
	Divers	1.26 (0.13-2.38)	-3.13 (-5.52- -0.74)	0.43*
	Procellariidae	1.43 (0.88-1.97)	-3.45 (-4.62- -2.28)	0.61***
	Procellariiformes	2.15 (1.69-2.60)	-4.95 (-5.95- -3.96)	0.78***
P6	Non-divers	1.21 (0.27-2.16)	-3.16 (-5.30- -1.02)	0.43*
	Divers	0.58 (-0.22-1.38)	-1.85 (-3.60- -0.09)	0.19
	Procellariidae	0.89 (0.34-1.44)	-2.47 (-3.69- -1.24)	0.36**
	Procellariiformes	1.77 (1.24-2.30)	-4.36 (-5.57- -3.15)	0.63***
P8	Non-divers	1.02 (-0.29-2.34)	-2.82 (-5.87-0.21)	0.17
	Divers	0.50 (-0.35-1.34)	-1.73 (-3.63—0.16)	0.10
	Procellariidae	0.74 (0.10-1.38)	-2.23 (-3.69- -0.76)	0.21*
	Procellariiformes	1.59 (1.08-2.10)	-4.11 (-5.30- -2.92)	0.60***
P10	Non-divers	1.58 (0.62-2.54)	-4.15 (-6.36- -1.94)	0.56**
	Divers	0.61 (0.08-1.4)	-1.97 (-3.16- -0.78)	0.45*
	Procellariidae	0.93 (0.46-1.41)	-2.68 (-3.76- -1.59)	0.46***
	Procellariiformes	1.69 (1.29-2.09)	-4.36 (-5.30- -3.41)	0.73***

*P<0.05 **P<0.01 ***P<0.001

Appendix 18b: The allometric relationship between feather length and rachis stiffness at 4 degrees at the base of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.76 (1.15-2.37)	-3.91 (-5.17- -2.65)	0.80**
	Divers	2.22 (0.53-3.90)	-4.95 (-8.35- -1.54)	0.52*
	Procellariidae	2.04 (1.29-2.80)	-4.55 (-6.08- -3.01)	0.62***
	Procellariiformes	2.59 (2.08-3.09)	-5.64 (-6.69- -4.58)	0.80***
P4	Non-divers	1.49 (0.75-2.22)	-3.51 (-5.10- -1.92)	0.67**
	Divers	1.68 (0.41-2.94)	-4.03 (-6.71- -1.35)	0.53*
	Procellariidae	1.68 (1.04-2.32)	-3.98 (-5.35- -2.60)	0.61***
	Procellariiformes	2.37 (1.87-2.86)	-5.41 (-6.49- -4.33)	0.78***
P6	Non-divers	1.29 (0.53-2.06)	-3.34 (-5.07- -1.60)	0.58**
	Divers	0.73 (-0.30-1.77)	-2.18 (-4.46-0.10)	0.18
	Procellariidae	1.00 (0.43-1.57)	-2.71 (-3.98- -1.44)	0.40*
	Procellariiformes	1.96 (1.42-2.51)	-4.80 (-6.04- -3.56)	0.67***
P8	Non-divers	1.03 (-0.24-2.29)	-2.85 (-5.77-0.07)	0.19
	Divers	1.04 (0.04-2.03)	-2.95 (-5.18- -0.72)	0.39*
	Procellariidae	1.45 (0.44-1.74)	-3.70 (-4.51- -1.56)	0.78***
	Procellariiformes	1.80 (1.32-2.28)	-4.61 (-5.73- -3.49)	0.69***
P10	Non-divers	1.64 (0.73-2.55)	-4.31 (-6.42- -2.21)	0.61**
	Divers	0.57 (0.01-1.13)	-1.91 (-3.17- -0.65)	0.38
	Procellariidae	0.92 (0.44-1.40)	-2.67 (-3.77- -1.58)	0.45**
	Procellariiformes	1.69 (1.27-2.12)	-4.36 (-5.36- -3.36)	0.71***

*P<0.05 **P<0.01 ***P<0.001

Appendix 19a: The allometric relationship between feather length and rachis stiffness at 8 degrees at the base of a dorsally oriented feather.

Feather	**Group**	**Slope (95% CI)**	**Intercept (95% CI)**	**R^2**
P2	Non-divers	1.99 (1.47-2.50)	-4.12 (-5.18- -3.06)	0.88***
	Divers	2.46 (0.71-4.21)	-5.16 (-8.70- -1.62)	0.56*
	Procellariidae	2.27 (1.52-3.02)	-4.73 (-6.26- -3.20)	0.67***
	Procellariiformes	2.56 (2.12-3.00)	-5.31 (-6.23- -4.39)	0.84***
P4	Non-divers	1.57 (0.96-2.18)	-3.45 (-4.77- -2.12)	0.77***
	Divers	1.28 (0.21-2.35)	-2.87 (-5.14- -0.60)	0.47*
	Procellariidae	1.43 (0.91-1.95)	-3.16 (-4.28- -2.04)	0.63***
	Procellariiformes	2.07 (1.64-2.51)	-4.49 (-5.44- -3.55)	0.78***
P6	Non-divers	1.31 (0.33-2.28)	-3.07 (-5.28- -0.87)	0.45*
	Divers	0.64 (-0.11-1.39)	-1.67 (-3.33- -0.01)	0.27
	Procellariidae	0.95 (0.41-1.49)	-2.30 (-3.50- -1.09)	0.4***
	Procellariiformes	1.77 (1.25-2.28)	-4.05 (-5.22- -2.87)	0.64***
P8	Non-divers	1.14 (-0.15-2.44)	-2.81 (-5.81-0.19)	0.23
	Divers	0.63 (-0.11-1.36)	-1.71 (-3.36- -0.06)	0.28
	Procellariidae	0.84 (0.25-1.44)	-2.16 (-3.52- -0.80)	0.30**
	Procellariiformes	1.63 (1.16-2.11)	-3.91 (-5.01- -2.80)	0.65***
P10	Non-divers	1.63 (0.74-2.51)	-3.96 (-6.01- -1.91)	0.62**
	Divers	0.69 (0.25-1.13)	-1.85 (-2.84- -0.86)	0.62**
	Procellariidae	1.00 (0.56-1.43)	-2.52 (-3.51- -1.54)	0.54***
	Procellariiformes	1.71 (1.33-2.08)	-4.10 (-4.97- -3.22)	0.76***

*P<0.05 **P<0.01 ***P<0.001

Appendix 19b: The allometric relationship between feather length and rachis stiffness at 8 degrees at the base of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.90 (1.36-2.43)	-3.90 (-5.01- -2.80)	0.86***
	Divers	2.37 (0.64-4.11)	-4.95 (-8.46- -1.44)	0.54*
	Procellariidae	2.18 (1.43-2.93)	-4.51 (-6.04- -2.99)	0.66***
	Procellariiformes	2.58 (2.12-3.03)	-5.31 (-6.27- -4.36)	0.83***
P4	Non-divers	1.59 (0.96-2.21)	-3.44 (-4.80- -2.08)	0.76***
	Divers	1.55 (0.33-2.77)	-3.42 (-6.01- -0.84)	0.50*
	Procellariidae	1.62 (1.03-2.20)	-3.53 (-4.79- -2.28)	0.63***
	Procellariiformes	2.27 (1.81-2.74)	-4.89 (-5.91- -3.87)	0.79***
P6	Non-divers	1.43 (0.63-2.23)	-3.35 (-5.16- -1.54)	0.61**
	Divers	0.77 (-0.19-1.74)	-1.95 (-4.06-0.17)	0.25*
	Procellariidae	1.06 (0.51-1.61)	-2.54 (-3.77- -1.31)	0.45***
	Procellariiformes	1.97 (1.45-2.50)	-4.51 (-5.70- -3.31)	0.69***
P8	Non-divers	1.17 (-0.07-2.41)	-2.87 (-5.75-0.001)	0.26
	Divers	0.82 (0.09-1.56)	-2.16 (-3.81- -0.50)	0.43*
	Procellariidae	0.98 (0.41-1.55)	-2.47 (-3.78- -1.17)	0.39***
	Procellariiformes	1.74 (1.28-2.20)	-4.16 (-5.23- -3.09)	0.69***
P10	Non-divers	1.70 (0.92-2.48)	-4.15 (-5.95- -2.35)	0.70***
	Divers	0.52 (0.06-0.97)	-1.45 (-2.48- -0.45)	0.44*
	Procellariidae	0.88 (0.45-1.32)	-2.28 (-3.27- -1.28)	0.47***
	Procellariiformes	1.69 (1.26-2.12)	-4.03 (-5.03- -3.02)	0.70***

*P<0.05 **P<0.01 ***P<0.001

Appendix 20a: The allometric relationship between feather length and rachis stiffness at 12 degrees at the base of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	2.05 (1.13-2.96)	-4.16 (-6.03- -2.28)	0.71***
	Divers	2.23 (0.62-3.84)	-4.58 (-7.85- -1.31)	0.55***
	Procellariidae	2.17 (1.40-2.93)	-4.42 (-5.99- -2.86)	0.64***
	Procellariiformes	2.37 (1.91-2.83)	-4.83 (-5.78- -3.87)	0.81***
P4	Non-divers	1.72 (0.86- -1.83)	-3.70 (-5.56- -1.83)	0.66**
	Divers	1.09 (-0.01-2.19)	-2.32 (-4.65-0.02)	0.36
	Procellariidae	1.33 (0.73-1.93)	-2.84 (-4.13- -1.55)	0.52***
	Procellariiformes	2.03 (1.55-2.51)	-4.29 (-5.34- -3.24)	0.74***
P6	Non-divers	1.41 (0.47-2.36)	-3.19 (-5.33- -1.04)	0.51**
	Divers	0.50 (-0.33-1.32)	-1.22 (-3.03-0.60)	0.11
	Procellariidae	0.88 (0.32-1.45)	-2.02 (-3.29- -0.76)	0.34***
	Procellariiformes	1.80 (1.27-2.34)	-4.01 (-5.23- -2.79)	0.64***
P8	Non-divers	1.16 (-0.08-2.39)	-2.71 (-5.56-0.14)	0.26
	Divers	0.52 (-0.28-1.32)	-1.33 (-3.13-0.47)	0.15
	Procellariidae	0.77 (0.18-1.37)	-1.85 (-3.22- -0.49)	0.25*
	Procellariiformes	1.62 (1.13-2.11)	-3.74 (-4.89- -2.60)	0.63***
P10	Non-divers	1.68 (0.85-2.50)	-3.94 (-5.84- -2.03)	0.67**
	Divers	0.59 (0.11-1.08)	-1.49 (-2.58- -0.40)	0.48*
	Procellariidae	0.94 (0.50-1.39)	-2.46 (-3.28- -1.25)	0.50***
	Procellariiformes	1.68 (1.29-2.07)	-3.89 (-4.80- -2.99)	0.74***

*P<0.05 **P<0.01 ***P<0.001

Appendix 20b: The allometric relationship between feather length and rachis stiffness at 12 degrees at the base of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	2.05 (1.34-2.76)	-4.14 (-5.61- -2.68)	0.81***
	Divers	2.25 (0.52-3.99)	-4.56 (-8.07- -1.05)	0.51*
	Procellariidae	2.16 (1.41-2.91)	-4.37 (-5.91- -2.83)	0.65***
	Procellariiformes	2.39 (1.95-2.83)	-4.82 (-5.74- -3.91)	0.82***
P4	Non-divers	1.36 (0.70-2.03)	-2.80 (-4.25- -1.35)	0.67**
	Divers	1.33 (0.07-2.60)	-2.82 (-5.50- -0.13)	0.39*
	Procellariidae	1.40 (0.79-2.01)	-2.92 (-4.23- -1.61)	0.54***
	Procellariiformes	2.15 (1.66-2.64)	-4.47 (-5.56- -3.39)	0.75***
P6	Non-divers	1.42 (0.50-2.34)	-3.19 (-5.27- -1.11)	0.53**
	Divers	0.65 (-0.35-1.65)	-1.51 (3.71-0.69)	0.14
	Procellariidae	0.97 (0.38-1.57)	-2.19 (-3.52- -0.86)	0.36**
	Procellariiformes	1.93 (1.37-2.48)	-4.25 (-5.52- -2.98)	0.65***
P8	Non-divers	1.21 (0.07-2.35)	-2.82 (-5.46- -0.81)	0.32*
	Divers	0.66 (-0.09-1.41)	-1.62 (-3.31- 0.07)	0.29
	Procellariidae	0.87 (0.32-1.42)	-2.06 (-3.32- -0.81)	0.35*
	Procellariiformes	1.68 (1.22-2.15)	-3.86 (-4.94- -2.77)	0.67***
P10	Non-divers	1.67 (0.79-2.55)	-3.91 (-5.93- -1.88)	0.64**
	Divers	0.42 (-0.03-0.87)	-1.07 (-2.09- -0.06)	0.32
	Procellariidae	0.82 (0.35-1.29)	-1.95 (-3.03- -0.88)	0.39***
	Procellariiformes	1.61 (1.18-2.05)	-3.69 (-4.71- -2.67)	0.68***

*P<0.05 **P<0.01 ***P<0.001

Appendix 21a: The allometric relationship between feather length and rachis stiffness at 4 degrees at the middle of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.87 (1.19-2.56)	-4.67 (-6.08- -3.27)	0.79***
	Divers	2.22 (1.27-3.16)	-5.47 (-7.39- -3.56)	0.79***
	Procellariidae	2.10 (1.57-2.63)	-5.18 (-6.27- -4.10)	0.78***
	Procellariiformes	2.38 (2.05-2.71)	-5.76 (-6.45- -5.06)	0.89***
P4	Non-divers	1.80 (1.45-2.16)	-4.74 (-5.50- -3.97)	0.93***
	Divers	1.38 (0.27-2.49)	-3.94 (-6.30- -1.57)	0.49*
	Procellariidae	1.63 (1.10-2.16)	-4.41 (-5.56- -3.27)	0.68***
	Procellariiformes	2.22 (1.81-2.63)	-5.65 (-6.54- -4.75)	0.82***
P6	Non-divers	1.77 (1.21-2.33)	-4.89 (-6.16- -3.63)	0.83***
	Divers	1.26 (0.61-1.90)	-3.79 (-5.22- -2.37)	0.72**
	Procellariidae	1.48 (1.10-1.87)	-4.26 (-5.12- -2.37)	0.77***
	Procellariiformes	2.13 (1.77-2.49)	-5.66 (-6.49- --6.49)	0.84***
P8	Non-divers	1.73 (1.04-2.43)	-4.96 (-6.49- -4.84)	0.76***
	Divers	1.10 (0.58-1.63)	-3.55 (-4.73- -2.36)	0.75***
	Procellariidae	1.32 (0.95-1.69)	-4.02 (-4.87- -3.17)	0.74***
	Procellariiformes	1.98 (1.62-2.34)	-5.51 (-6.35- -4.66)	0.82***
P10	Non-divers	1.99 (1.36-2.62)	-5.67 (-7.12- -4.21)	0.83***
	Divers	1.18 (0.87-1.49)	-3.80 (-4.51- -3.09)	0.91***
	Procellariidae	1.42 (1.09-1.74)	-4.35 (-5.09- -3.60)	0.81***
	Procellariiformes	1.86 (1.60-2.13)	-5.33 (-5.95- -4.72)	0.89***

*P<0.05 **P<0.01 ***P<0.001

Appendix 21b: The allometric relationship between feather length and rachis stiffness at 4 degrees at the middle of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.74 (1.16-2.32)	-4.36 (-5.55- -3.16)	0.82***
	Divers	2.44 (1.37-3.51)	-5.89 (-8.06- -3.72)	0.78***
	Procellariidae	2.15 (1.58-2.72)	-5.25 (-6.40- -4.09)	0.77***
	Procellariiformes	2.45 (2.09-2.82)	-5.88 (-6.65- -5.12)	0.87***
P4	Non-divers	1.91 (1.49-2.33)	-4.93 (-5.85- -4.01)	0.91***
	Divers	2.08 (1.18-2.98)	-5.38 (-7.30- -3.46)	0.78***
	Procellariidae	2.06 (1.64 (2.50)	-5.30 (-6.24-4.36)	0.84***
	Procellariiformes	2.49 (2.17-2.81)	-6.20 (-6.91- -5.49)	0.90***
P6	Non-divers	1.77 (1.32-2.23)	-4.88 (-5.90- -3.85)	0.89***
	Divers	1.27 (0.68-1.86)	-3.81 (-5.11- -2.51)	0.76**
	Procellariidae	1.49 (1.15-1.83)	-4.26 (-5.02- -3.50)	0.81***
	Procellariiformes	2.16 (1.81-2.51)	-5.72 (-6.53- -4.92)	0.85***
P8	Non-divers	1.69 (1.05-2.33)	-4.83 (-6.32- -3.35)	0.77***
	Divers	1.33 (0.87-1.79)	-4.04 (-5.08- -3.01)	0.85***
	Procellariidae	1.47 (1.14-1.79)	-4.34 (-5.08- -3.60)	0.82***
	Procellariiformes	2.00 (1.71-2.29)	-5.53 (-6.21- -4.85)	0.88***
P10	Non-divers	2.03 (1.54-2.52)	-5.76 (-6.88- -4.63)	0.90***
	Divers	1.17 (0.95-1.39)	-3.79 (-4.28- -3.30)	0.95***
	Procellariidae	1.44 (1.16-1.72)	-4.39 (-5.02- -3.75)	0.86***
	Procellariiformes	1.86 (1.62-2.09)	-5.31 (-5.86- -4.76)	0.91***

*P<0.05 **P<0.01 ***P<0.001

Appendix 22a: The allometric relationship between feather length and rachis stiffness at 12 degrees at the middle of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.88 (1.15-2.61)	-4.28 (-5.78- -2.78)	0.77***
	Divers	2.19 (1.19-3.19)	-4.98 (-7.01- -2.96)	0.76**
	Procellariidae	2.07 (1.54-2.60)	-4.70 (-5.79- -3.61)	0.78***
	Procellariiformes	2.27 (1.94-2.61)	-5.11 (-5.81- -4.41)	0.88***
P4	Non-divers	1.87 (1.49-2.25)	-4.48 (-5.30- -3.65)	0.93***
	Divers	1.52 (0.82-2.21)	-3.75 (-5.23- -2.26)	0.76**
	Procellariidae	1.68 (1.33-2.02)	-4.07 (-4.81- -3.33)	0.85***
	Procellariiformes	2.16 (1.85-2.48)	-5.10 (-5.79- -4.42)	0.88***
P6	Non-divers	1.87 (1.31-2.42)	-4.69 (-5.94- -3.44)	0.85***
	Divers	1.20 (0.59-1.81)	-3.26 (-4.60- -1.92)	0.72**
	Procellariidae	1.48 (1.10-1.86)	-3.84 (-4.70- -2.99)	0.78***
	Procellariiformes	2.14 (1.77-2.50)	-5.27 (-6.10- -4.44)	0.84***
P8	Non-divers	1.82 (1.15-2.49)	-4.75 (-6.29- -3.21)	0.79***
	Divers	1.03 (0.51-1.54)	-2.95 (-4.10- -1.80)	0.73**

	Procellariidae	1.29 (0.91-1.66)	-3.53 (-4.39- -2.67)	0.73***
	Procellariiformes	1.98 (1.61-2.36)	-5.10 (-5.97- -4.23)	0.81***
P10	Non-divers	2.04 (1.56-2.53)	-5.37 (-6.49- -4.25)	0.90***
	Divers	1.10 (0.83-1.36)	-3.19 (-3.78- -2.60)	0.92***
	Procellariidae	1.38 (1.08-1.68)	-3.83 (-4.52- -3.14)	0.83***
	Procellariiformes	1.84 (1.58-2.10)	-4.85 (-5.45- -4.25)	0.89***

*P<0.05 **P<0.01 ***P<0.001

Appendix 22b: The allometric relationship between feather length and rachis stiffness at 12 degrees at the middle of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.96 (1.53-2.39)	-4.37 (-5.26- -3.49)	0.91***
	Divers	2.35 (1.25-3.45)	-5.25 (-7.48- -3.02)	0.75**
	Procellariidae	2.20 (1.69-2.70)	-4.89 (-5.92- -3.86)	0.81***
	Procellariiformes	2.56 (2.22-2.90)	-5.63 (-6.34- -4.92)	0.90***
P4	Non-divers	2.02 (1.62-2.41)	-4.72 (-5.58- -3.86)	0.93***
	Divers	1.81 (1.01-2.61)	-4.31 (-6.01- -2.61)	0.78**
	Procellariidae	1.92 (1.54-2.31)	-4.53 (-5.35- -3.71)	0.85***
	Procellariiformes	2.40 (2.09-2.71)	-5.52 (-6.20- -4.83)	0.90***
P6	Non-divers	1.88 (1.40-2.37)	-4.66 (-5.75- -3.57)	0.88***
	Divers	1.17 (0.57-1.77)	-3.10 (-4.43- -1.78)	0.72**
	Procellariidae	1.45 (1.09-1.82)	-3.70 (-4.52- -2.89)	0.78***
	Procellariiformes	2.13 (1.77-2.49)	-5.17 (-5.99- -4.35)	0.84***
P8	Non-divers	1.88 (1.27-2.49)	-4.81 (-6.22- -3.40)	0.83***
	Divers	1.27 (0.82-1.71)	-3.42 (-4.43- -2.42)	0.85***
	Procellariidae	1.47 (1.14-1.80)	-3.87 (-4.62- -3.12)	0.82***
	Procellariiformes	2.00 (1.70-2.29)	-5.05 (-5.72- -4.37)	0.88***
P10	Non-divers	2.14 (1.64-2.65)	-5.56 (-6.71- -4.40)	0.90***
	Divers	1.11 (0.84-1.38)	-3.17 (-3.79- -2.56)	0.92***
	Procellariidae	1.42 (1.10-1.74)	-3.89 (-4.62- -3.16)	0.82***
	Procellariiformes	1.83 (1.58-2.08)	-4.78 (-5.36- -4.19)	0.89***

*P<0.05 **P<0.01 ***P<0.001

Appendix 23a: The allometric relationship between feather length and rachis stiffness at 4 degrees at the tip of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.96 (1.22-2.70)	-5.33 (-6.76- -4.55)	0.78***
	Divers	2.53 (1.73-3.32)	-6.55 (-8.16- -4.94)	0.87***
	Procellariidae	2.28 (1.78-2.78)	-6.02 (-7.03- -5.00)	0.83***
	Procellariiformes	2.46 (2.12-2.80)	-6.39 (-7.10- -5.69)	0.89***
P4	Non-divers	2.00 (1.49-2.51)	-5.65 (-6.76- -4.55)	0.89***
	Divers	1.98 (1.54-2.43)	-5.65 (-6.60- -4.70)	0.93***
	Procellariidae	2.01 (1.72-2.29)	-5.69 (-6.30- -5.08)	0.92***
	Procellariiformes	2.39 (2.15-2.62)	-6.49 (-7.01- -5.97)	0.94***
P6	Non-divers	2.04 (1.63-2.45)	-5.00 (-6.92- -5.07)	0.93***
	Divers	1.45 (1.06-1.85)	-4.67 (-5.53- -3.81)	0.90***
	Procellariidae	1.66 (1.39-1.93)	-5.13 (-5.73- -4.53)	0.90***
	Procellariiformes	2.21 (1.91-2.51)	-6.34 (-7.01- -5.66)	0.90***
P8	Non-divers	2.15 (1.61-2.69)	-6.41 (-7.66- -5.16)	0.89***
	Divers	1.45 (1.02-1.86)	-4.76 (-5.70- -3.83)	0.89***
	Procellariidae	1.64 (1.32-1.95)	-5.21 (-5.93- -4.49)	0.86***
	Procellariiformes	2.15 (1.83-2.46)	-6.38 (-7.12- -5.64)	0.88***
P10	Non-divers	2.20 (1.68-2.71)	-6.63 (-7.82- -5.45)	0.90***
	Divers	1.58 (1.31-1.84)	-5.15 (-5.75- -4.56)	0.96***
	Procellariidae	1.73 (1.45-2.01)	-5.54 (-6.17- -4.90)	0.90***
	Procellariiformes	2.05 (1.84-2.26)	-6.25 (-6.75- -5.76)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Appendix 23b: The allometric relationship between feather length and rachis stiffness at 4 degrees at the tip of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	2.00 (1.43-2.57)	-5.37 (-6.55- -4.20)	0.86***
	Divers	2.46 (1.61-3.32)	-6.38 (-8.12- -4.64)	0.85***
	Procellariidae	2.27 (1.81-2.73)	-5.95 (-6.89- -5.02)	0.85***
	Procellariiformes	2.46 (2.13-2.78)	-6.36 (-7.04- -5.68)	0.90***
P4	Non-divers	1.93 (1.49-2.37)	-5.45 (-6.41- -4.50)	0.91***
	Divers	2.04 (1.49-2.60)	-5.74 (-6.92- -4.55)	0.90***
	Procellariidae	2.03 (1.73-2.34)	-5.69 (-6.35- -5.03)	0.91***
	Procellariiformes	2.38 (2.14-2.62)	-6.42 (-6.95- -5.90)	0.94***
P6	Non-divers	1.93 (1.58-2.27)	-5.65 (-6.44- -4.87)	0.94***
	Divers	1.57 (1.13-2.01)	-4.88 (-5.84- -3.92)	0.90***
	Procellariidae	1.72 (1.47-1.97)	-5.19 (-5.75- -4.64)	0.92***
	Procellariiformes	2.24 (1.96-2.52)	-6.34 (-6.98- -5.60)	0.91***
P8	Non-divers	1.98 (1.47-2.49)	-5.94 (-7.12- -4.76)	0.88***
	Divers	1.59 (1.22-1.95)	-5.05 (-5.87- -4.23)	0.93***
	Procellariidae	1.72 (1.46-1.98)	-5.33 (-5.93- -4.74)	0.91***
	Procellariiformes	2.14 (1.89-2.39)	-6.29 (-6.87- -5.71)	0.92***
P10	Non-divers	2.20 (1.82-2.57)	-6.59 (-7.46- -5.73)	0.95***
	Divers	1.29 (1.02-1.56)	-4.47 (-5.07- -3.86)	0.94***
	Procellariidae	1.54 (1.26-1.83)	-5.06 (-5.71- -4.41)	0.87***
	Procellariiformes	1.92 (1.69-2.14)	-5.89 (-6.41- -5.37)	0.92***

*P<0.05 **P<0.01 ***P<0.001

Appendix 24a: The allometric relationship between feather length and rachis stiffness at 12 degrees at the tip of a dorsally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	1.91 (1.20-2.63)	-4.89 (-6.36- -3.42)	0.78***
	Divers	2.39 (1.53-3.25)	-5.88 (-7.62- -4.15)	0.84***
	Procellariidae	2.17 (1.68-2.65)	-5.42 (-6.41- -4.43)	0.82***
	Procellariiformes	2.34 (2.00-2.68)	-5.79 (-6.49- -5.08)	0.88***
P4	Non-divers	2.06 (1.55-2.56)	-5.44 (-6.54- -4.34)	0.89***
	Divers	1.90 (1.46-2.34)	-5.10 (-6.04- -4.16)	0.93***
	Procellariidae	1.96 (1.68-2.24)	-5.22 (-5.82- -4.61)	0.92***
	Procellariiformes	2.30 (2.06-2.54)	-5.94 (-6.47- -5.42)	0.94***
P6	Non-divers	2.00 (1.65-2.36)	-5.55 (-6.35- -4.74)	0.94***
	Divers	1.46 (1.06-1.87)	-4.34 (-5.23- -3.45)	0.90***
	Procellariidae	1.65 (1.40-1.91)	-4.75 (-5.32- -4.18)	0.91***
	Procellariiformes	2.18 (1.90-2.47)	-5.92 (-6.57- -5.26)	0.90***
P8	Non-divers	2.17 (1.56-2.78)	-6.10 (-7.52- -4.69)	0.86***
	Divers	1.34 (0.89-1.78)	-4.14 (-5.14- -3.13)	0.86***
	Procellariidae	1.55 (1.19-1.91)	-4.66 (-5.48- -3.83)	0.81***
	Procellariiformes	2.11 (1.75-2.47)	-5.93 (-6.77- -5.10)	0.85***
P10	Non-divers	2.09 (1.63-2.54)	-6.00 (-7.06- -4.95)	0.91***
	Divers	1.53 (1.34-1.72)	-4.61 (-5.09- -4.24)	0.98***
	Procellariidae	1.66 (1.42-1.91)	-5.00 (-5.56- -4.44)	0.91***
	Procellariiformes	2.02 (1.81-2.22)	-5.79 (-6.27- -5.30)	0.94***

*P<0.05 **P<0.01 ***P<0.001

Appendix 24b: The allometric relationship between feather length and rachis stiffness at 12 degrees at the tip of a ventrally oriented feather.

Feather	Group	Slope (95% CI)	Intercept (95% CI)	R^2
P2	Non-divers	2.11 (1.49-2.72)	-5.15 (-6.41- -3.88)	0.86***
	Divers	2.38 (1.58-3.19)	-5.75 (-7.38- -4.12)	0.86***
	Procellariidae	2.27 (1.83-2.70)	-5.49 (-6.38- -4.61)	0.86***
	Procellariiformes	2.46 (2.04-2.87)	-5.92 (-6.77- -5.07)	0.85***
P4	Non-divers	2.06 (1.60-2.52)	-5.27 (-6.28- -4.27)	0.91***
	Divers	1.94 (1.47-2.41)	-5.03 (-6.03- -4.02)	0.92***
	Procellariidae	2.00 (1.72-2.27)	-5.14 (-5.74- -4.55)	0.92***
	Procellariiformes	2.33 (2.10-2.56)	-5.85 (-6.36- -5.35)	0.94***
P6	Non-divers	2.07 (1.69-2.45)	-5.51 (-6.37- -4.65)	0.94***
	Divers	1.52 (1.13-1.91)	-4.29 (-5.15- -3.44)	0.91***
	Procellariidae	1.73 (1.47-1.99)	-4.73 (-5.31- -4.17)	0.91***
	Procellariiformes	2.23 (1.96-2.50)	-5.84 (-6.46- -5.22)	0.91***
P8	Non-divers	2.24 (1.54-2.94)	-6.05 (-7.68- -4.42)	0.84***
	Divers	1.58 (1.24-1.92)	-4.54 (-5.31- -3.77)	0.94***
	Procellariidae	1.78 (1.45-2.11)	-5.00 (-5.75- -4.25)	0.87***
	Procellariiformes	2.16 (1.89-2.43)	-5.86 (-6.48- -5.23)	0.91***
P10	Non-divers	2.37 (1.96-2.77)	-6.53 (-7.47- -5.59)	0.94***
	Divers	1.33 (1.06-1.60)	-4.33 (-4.71- -3.50)	0.94***
	Procellariidae	1.62 (1.31-1.93)	-4.78 (-5.50- -4.07)	0.86***
	Procellariiformes	1.94 (1.72-2.17)	-5.50 (-6.03- -3.98)	0.92***

*P<0.05 **P<0.01 ***P<0.001

Appendix 25: The slope comparison of rachis stiffness relative to feather length between the diving birds and the non-diving birds.

	Sum Sq	Mean Sq	F value	Pr (>F)
	Base 4° Upstroke			
Feather length	<0.0001	<0.0001	0,71	0,41
Group	<0.0001	<0.0001	0,04	0,85
Featherlength:Group	<0.0001	<0.0001	2,43	0,05
	Base 4° Downstroke			
Feather length	<0.0001	<0.0001	3,02	0,1
Group	<0.0001	<0.0001	0,36	0,56
Featherlength:Group	<0.0001	<0.0001	6,2	0,02
	Base 8° Upstroke			
Feather length	<0.0001	<0.0001	0,45	0,51
Group	<0.0001	<0.0001	0,74	0,4
Featherlength:Group	<0.0001	<0.0001	2,43	0,14
	Base 8° Downstroke			

Feather length	<0.0001	<0.0001	0,97	0,34
Group	<0.0001	<0.0001	0,27	0,61
Featherlength:Group	<0.0001	<0.0001	2,46	0,14
Base 12° Upstroke				
Feather length	<0.0001	<0.0001	0,19	0,67
Group	<0.0001	<0.0001	3,37	0,08
Featherlength:Group	<0.0001	<0.0001	0,8	0,39
Base 12° Downstroke				
Feather length	<0.0001	<0.0001	0	0,96
Group	<0.0001	<0.0001	3,92	0,07
Featherlength:Group	<0.0001	<0.0001	0,42	0,53
Middle 4° Upstroke				
Feather length	<0.0001	<0.0001	0,01	0,93
Group	<0.0001	<0.0001	0,63	0,44
Featherlength:Group	<0.0001	<0.0001	0,87	0,36
Middle 4° Downstroke				
Feather length	<0.0001	<0.0001	0,04	0,84
Group	<0.0001	<0.0001	0,35	0,56
Featherlength:Group	<0.0001	<0.0001	2,77	0,12
Middle 8° Upstroke				
Feather length	<0.0001	<0.0001	0,02	0,9
Group	<0.0001	<0.0001	0,01	0,92
Featherlength:Group	<0.0001	<0.0001	0,08	0,78
Middle 8° Downstroke				
Feather length	<0.0001	<0.0001	1,2	0,29
Group	<0.0001	<0.0001	0,4	0,54
Featherlength:Group	<0.0001	<0.0001	0,52	0,48
Middle 12° Upstroke				
Feather length	<0.0001	<0.0001	1,18	0,29
Group	<0.0001	<0.0001	0,02	0,89
Featherlength:Group	<0.0001	<0.0001	2,91	0,11
Middle 12° Downstroke				
Feather length	<0.0001	<0.0001	1,68	0,26
Group	<0.0001	<0.0001	0,06	0,81
Featherlength:Group	<0.0001	<0.0001	3,34	0,09
Tip 4° Upstroke				
Feather length	<0.0001	<0.0001	8,46	0,01
Group	<0.0001	<0.0001	0,07	0,8
Featherlength:Group	<0.0001	<0.0001	0,17	0,74
Tip 4° Downstroke				
Feather length	<0.0001	<0.0001	4,38	0,05
Group	<0.0001	<0.0001	3,27	0,09
Featherlength:Group	<0.0001	<0.0001	21,11	0
Tip 8° Upstroke				

Feather length	<0.0001	<0.0001	0,02	0,9
Group	<0.0001	<0.0001	1,8	0,2
Featherlength:Group	<0.0001	<0.0001	0,11	0,75
Tip 8° Downstroke				
Feather length	<0.0001	<0.0001	3,95	0,06
Group	<0.0001	<0.0001	2,24	0,15
Featherlength:Group	<0.0001	<0.0001	5,13	0,04
Tip 12° Upstroke				
Feather length	<0.0001	<0.0001	3,01	0,1
Group	<0.0001	<0.0001	0,1	0,75
Featherlength:Group	<0.0001	<0.0001	1,82	0,2
Tip 12° Downstroke				
Feather length	<0.0001	<0.0001	3,01	0,1
Group	<0.0001	<0.0001	0,1	0,75
Featherlength:Group	<0.0001	<0.0001	1,82	1,2

Appendix 26a: The allometric relationship between body mass and feather stiffness at 4 degrees of a dorsally oriented feathers.

Section	Group	Slope 95% CI	Intercept 95% CI	R^2
Tip	Non-divers	0.62 (0.48-0.76)	-2.31 (-2.68- -1.94)	0.91***
	Divers	0.76 (0.58-0.95)	-2.85 (-3.35- -2.35)	0.92***
	Procellariidae	0.66 (0.51-0.81)	-2.48 (-2.87- -2.09)	0.82***
	Procellariiformes	0.67 (0.60-0.74)	-2.49 (-2.70- -2.28)	0.93***
Middle	Non-divers	0.59 (0.44-0.68)	-1.65 (-1.97- -1.34)	0.92***
	Divers	0.60 (0.32-0.88)	-1.97 (-2.73- -1.21)	0.76***
	Procellariidae	0.55 (0.38-0.72)	-1.72 (-2.18- -1.26)	0.70***
	Procellariiformes	0.63 (0.54-0.72)	-1.89 (-2.15- -1.63)	0.88***
Base	Non-divers	0.45 (0.25-0.66)	-0.86 (-1.40- -0.32))	0.70***
	Divers	0.41 (0.05-0.76)	-0.93 (-1.90-0.03)	0.45***
	Procellariidae	0.41 (0.20-0.61)	-0.82 (-1.37- -0.28)	0.47***
	Procellariiformes	0.58 (0.45-0.70)	-1.21 (-1.56- -0.85)	0.77***

*P<0.05 **P<0.01 ***P<0.001

Appendix 26b: The allometric relationship between body mass and feather stiffness at 4 degrees of a ventrally oriented feathers.

Section	Group	Slope 95% CI	Intercept 95% CI	R^2
Tip	Non-divers	0.60 (0.50-0.71)	-2.20 (-2.49- -1.92)	0.94***
	Divers	0.76 (0.54-0.98)	-2.80 (-3.40- -2.20)	0.79***
	Procellariidae	0.65 (0.49-0.80)	-2.40 (-2.81- -1.98)	0.89***
	Procellariiformes	0.66 (0.58-0.74)	-2.40 (-2.62- -2.18)	0.94***
Middle	Non-divers	0.55 (0.45-0.64)	-1.60 (-1.85- -1.34)	0.94***
	Divers	0.70 (0.41-0.98)	-2.20 (-2.96- -1.43)	0.81***
	Procellariidae	0.58 (0.41-0.76)	-1.78 (-2.25- -1.31)	0.71***
	Procellariiformes	0.65 (0.55-0.74)	-1.91 (-2.17- -1.65)	0.89***
Base	Non-divers	0.62 (0.49-0.75)	-0.86 (-1.32- -0.40)	0.77***
	Divers	0.45 (0.22-0.70)	-1.19 (-2.41-0.03)	0.43*
	Procellariidae	0.50 (0.05-0.95)	-0.93 (-1.52- -0.34)	0.47***
	Procellariiformes	0.45 (0.28-0.63)	-1.32 (-1.69- -0.95)	0.78***

*P<0.05 **P<0.01 ***P<0.001

Appendix 27a: The allometric relationship between body mass and feather stiffness at 12 degrees of a dorsally oriented feathers.

Section	Group	Slope 95% CI	Intercept 95% CI	R^2
Tip	Non-divers	0.62 (0.48-0.75)	-1.95 (-2.31- -1.59)	0.91***
	Divers	0.74 (0.55-0.93)	-2.40 (-2.91- -1.88)	0.91***
	Procellariidae	0.65 (0.52-0.78)	-2.09 (-2.45- -1.74)	0.85***
	Procellariiformes	0.66 (0.59-0.73)	-2.09 (-2.29- -1.90)	0.94***
Middle	Non-divers	0.58 (0.46-0.70)	-1.30 (-1.61- -0.99)	0.92***
	Divers	0.59 (0.33-0.85)	-1.50 (-2.20- -0.80)	0.78***
	Procellariidae	0.56 (0.41-0.71)	-1.33 (-1.73- -0.92)	0.75***
	Procellariiformes	0.63 (0.54-0.71)	-1.46 (-1.70- -1.23)	0.90***
Base	Non-divers	0.50 (0.29-0.70)	-0.57 (-1.12- -0.04)	0.74***
	Divers	0.38 (0.04-0.72)	0.41 (-1.32-0.50)	0.44*
	Procellariidae	0.42 (0.24-0.61)	-0.46 (-0.94- -0.03)	0.55***
	Procellariiformes	0.57 (0.46-0.68)	-0.78 (-1.10- -0.43)	0.80***

*P<0.05 **P<0.01 ***P<0.001

Appendix 27b: The allometric relationship between body mass and feather stiffness at 12 degrees of a ventrally oriented feathers.

Section	Group	Slope 95% CI	Intercept 95% CI	R^2
Tip	Non-divers	0.65 (0.53-0.78)	-1.87 (-2.20- -1.55)	0.93***
	Divers	0.75 (0.55-0.95)	-2.28 (-2.83- -1.74)	0.91***
	Procellariidae	0.65 (0.52-0.78)	-2.09 (-2.45- -1.74)	0.85***
	Procellariiformes	0.66 (0.59-0.74)	-1.95 (-2.16- -1.74)	0.93***
Middle	Non-divers	0.60 (0.51-0.69)	-1.28 (-1.52- -1.04)	0.96***
	Divers	0.65 (0.38-0.92)	-1.59 (-2.31- -0.86)	0.8***
	Procellariidae	0.60 (0.44-0.75)	-1.35 (-1.76- -0.93)	0.77***
	Procellariiformes	0.65 (0.56-0.73)	-1.44 (-1.69- -1.20)	0.90***
Base	Non-divers	0.48 (0.31-0.64)	-0.49 (-0.92- -0.060	0.81***
	Divers	0.42 (0.03-0.81)	-0.48 (-1.54-0.58)	0.40*
	Procellariidae	0.43 (0.24-0.62)	-0.44 (-0.94-0.07)	0.54***
	Procellariiformes	0.58 (0.46-0.70)	-0.77 (-1.10- -0.43)	0.79***

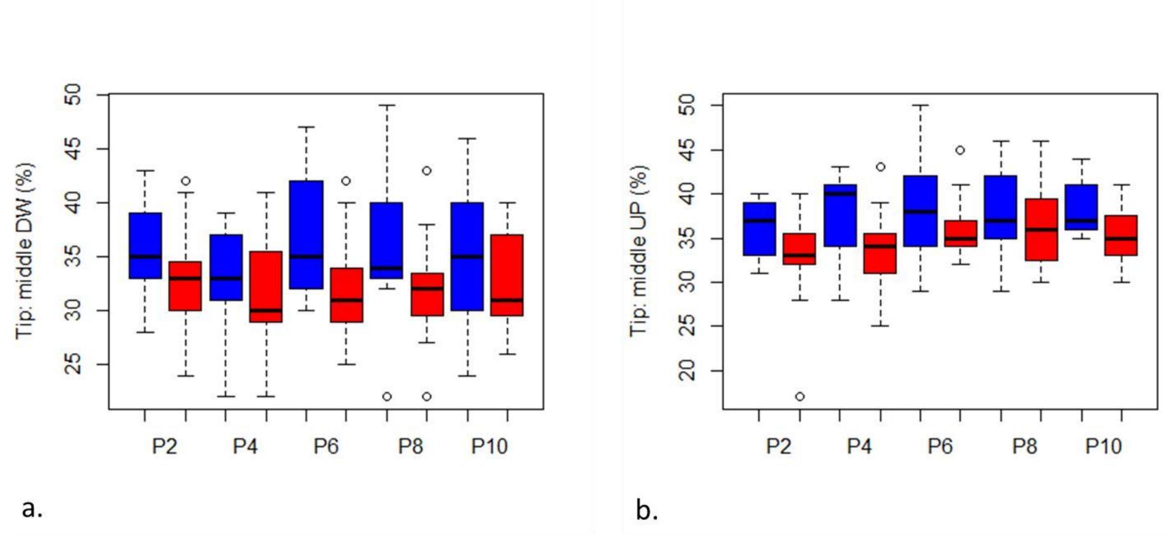
*P<0.05 **P<0.01 ***P<0.001

Appendix 28: The slope comparison of rachis stiffness relative to body mass between the diving birds and the non-diving birds.

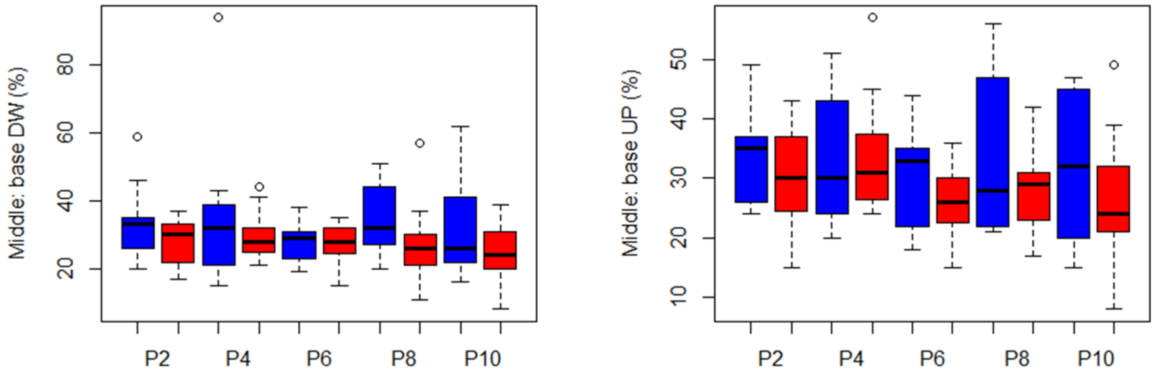
	Sum Sq	Mean Sq	F value	Pr (>F)
		Base 4° Upstroke		
Body mass	<0.0001	<0.0001	0,66	0,43
Group	<0.0001	<0.0001	0,12	0,74
Body mass: Group	<0.0001	<0.0001	4,64	0,05
		Base 4° Downstroke		
Body mass	<0.0001	<0.0001	7,01	0,02
Group	<0.0001	<0.0001	0,17	0,69
Body mass: Group	<0.0001	<0.0001	2,06	0,17
		Base 8° Upstroke		
Body mass	<0.0001	<0.0001	0,09	0,77
Group	<0.0001	<0.0001	0,55	0,47
Body mass: Group	<0.0001	<0.0001	3,1	0,1
		Base 8° Downstroke		
Body mass	<0.0001	<0.0001	0,01	0,94

Group	<0.0001	<0.0001	0,14	0,72
Body mass: Group	<0.0001	<0.0001	4,13	0,06
		Base 12° Upstroke		
Body mass	<0.0001	<0.0001	0,46	0,51
Group	<0.0001	<0.0001	3,73	0,07
Body mass: Group	<0.0001	<0.0001	0,81	0,38
		Base 12° Downstroke		
Body mass	<0.0001	<0.0001	1,33	0,27
Group	<0.0001	<0.0001	4,34	0,05
Body mass: Group	<0.0001	<0.0001	0,41	0,53
		Middle 4° Upstroke		
Body mass	<0.0001	<0.0001	0,26	0,62
Group	<0.0001	<0.0001	0,65	0,43
Body mass: Group	<0.0001	<0.0001	0,31	0,59
		Middle 4° Downstroke		
Body mass	<0.0001	<0.0001	0,93	0,35
Group	<0.0001	<0.0001	0,43	0,52
Body mass: Group	<0.0001	<0.0001	2,57	0,13
		Middle 8° Upstroke		
Body mass	<0.0001	<0.0001	0,06	0,81
Group	<0.0001	<0.0001	0,01	0,94
Body mass: Group	<0.0001	<0.0001	0,08	0,78
		Middle 8° Downstroke		
Body mass	<0.0001	<0.0001	0	0,98
Group	<0.0001	<0.0001	0,21	0,65
Body mass: Group	<0.0001	<0.0001	1,85	0,19
		Middle 12° Upstroke		
Body mass	<0.0001	<0.0001	0,25	0,62
Group	<0.0001	<0.0001	0,11	0,75
Body mass: Group	<0.0001	<0.0001	5,2	0,04
		Middle 12° Downstroke		
Body mass	<0.0001	<0.0001	0,08	0,76
Group	<0.0001	<0.0001	0	0,96
Body mass: Group	<0.0001	<0.0001	6,1	0,03
		Tip 4° Upstroke		
Body mass	<0.0001	<0.0001	4,09	0,06
Group	<0.0001	<0.0001	0,37	0,55
Body mass: Group	<0.0001	<0.0001	2,39	0,14

Tip 4° Downstroke				
Body mass	<0.0001	<0.0001	13,97	0
Group	<0.0001	<0.0001	2,2	0,16
Body mass: Group	<0.0001	<0.0001	6,45	0,02
Tip 8° Upstroke				
Body mass	<0.0001	<0.0001	0,19	0,67
Group	<0.0001	<0.0001	1,75	0,21
Body mass: Group	<0.0001	<0.0001	0,68	0,42
Tip 8° Downstroke				
Body mass	<0.0001	<0.0001	0,41	0,53
Group	<0.0001	<0.0001	1,43	0,25
Body mass: Group	<0.0001	<0.0001	9,1	0,01
Tip 12° Upstroke				
Body mass	<0.0001	<0.0001	0,09	0,77
Group	<0.0001	<0.0001	0,01	0,95
Body mass: Group	<0.0001	<0.0001	4,29	0,06
Tip 12° Downstroke				
Body mass	<0.0001	<0.0001	0,09	0,77
Group	<0.0001	<0.0001	0,01	0,95
Body mass: Group	<0.0001	<0.0001	4,29	0,06



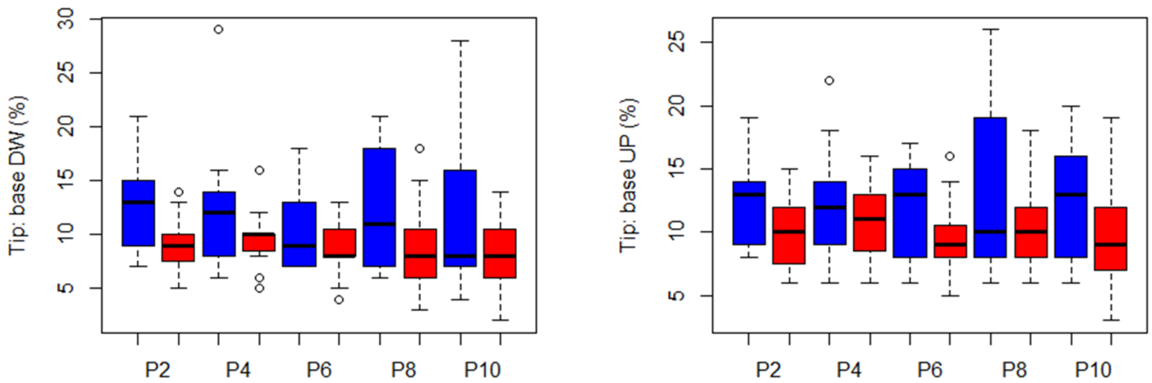
Appendix 29: The force required to bend the tip relative to the middle of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 4 °.



a.

b.

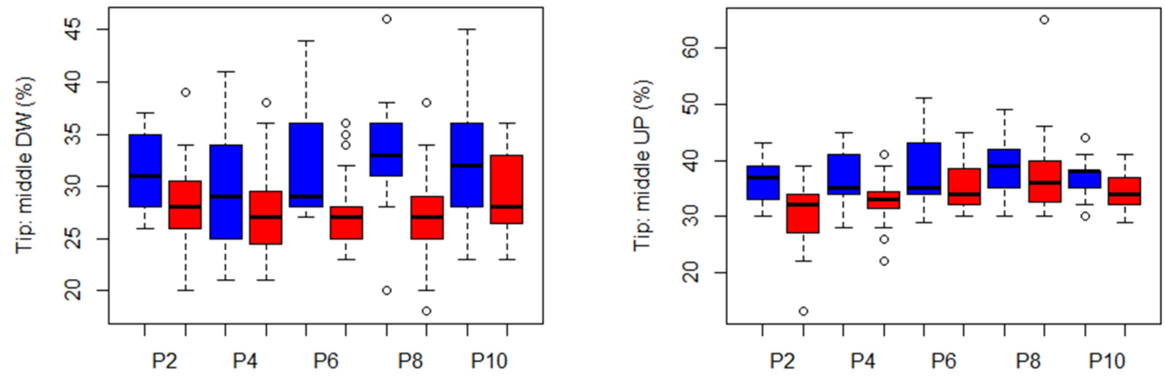
Appendix 30: The force required to bend the middle relative to the base of the feather 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 4 °.



a.

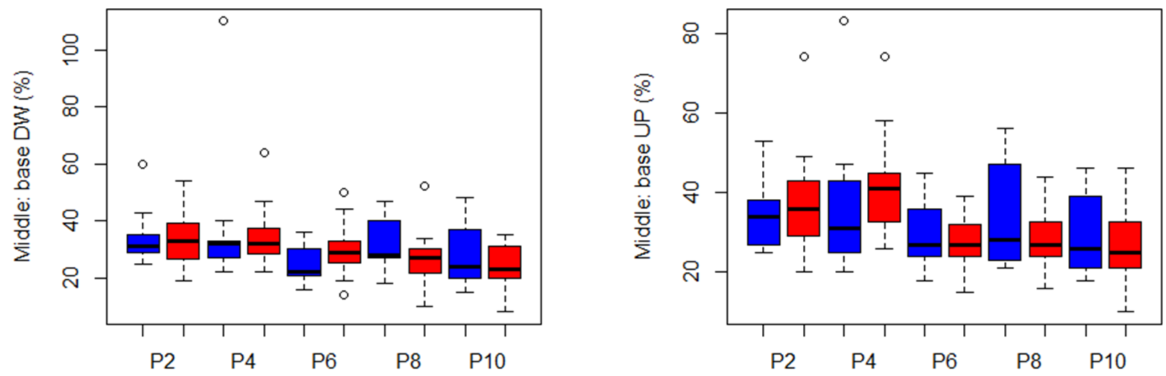
b.

Appendix 31: The force required to bend the tip relative to the base of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 4 °.



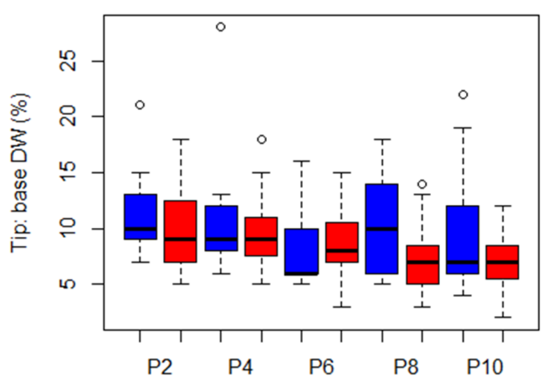
a. b.

Appendix 32: The force required to bend the tip relative to the middle of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 12°.

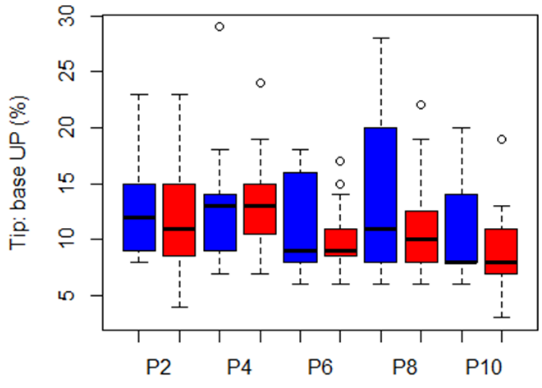


a. b.

Appendix 33: The force required to bend the middle relative to the base of the feather 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 12°.



a.



b.

Appendix 34: The force required to bend the tip relative to the base of the feather of 33 species of Procellariiformes showing divers (blue) being slightly greater than the non-divers (red); the ratios between middle and base when descending (a) showed lower percentages compared to ascending (b) at 12°.