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The influence of multi-species feeding associations on the foraging behaviour of Australasian gannets (*Morus serrator*) in the Hauraki Gulf, New Zealand

A thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology



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"It is good to have an end to journey toward; but it is the journey that matters, in the end."

- Ernest Hemingway

Abstract

In order to successfully capture prey in a challenging and physically demanding environment, Australasian gannets (*Morus serrator*) have developed a number of foraging strategies. Foremost among such strategies is the joining in formation of mixed species feeding associations (MSFA's) and the use of specialised plunge diving behaviours. This study sought to determine how gannets vary individual and group plunge diving behaviours in order to maximise the benefits and mitigate the risks associated with feeding in densely packed, highly active MSFA's.

Specifically this study's aims are to examine how variations in gannet dive heights, angles and completion rates are influenced by external stimuli, including weather parameters, oceanographic conditions and MSFA's species composition and behaviour. This study additionally seeks to examine what mixed and/or con-specific cues are associated with the formation of synchronous diving bouts, and determine its role as a form of local enhancement for gannets foraging in MSFA's.

Between March 2013 and June 2014, 45 independent boat based surveys were conducted aboard *Dolphin Explorer*, a 20m tour boat based in New Zealand's Hauraki Gulf. Using a Canon XH A1S high definition video camera, approximately 11.9hrs of MSFA video footage was collected, containing 5565 recorded gannet plunge dives. Variations in these dives, including their height, angle of entry, and synchronous timing were examined in context of environmental variables including wind speeds, sea surface temperatures, and Beaufort sea states as well as against MSFA variables including the abundance of other foraging gannets, the abundance and behaviour of common dolphins (*Delphinus* sp.), and the presence of other species including shearwaters (*Puffinus* spp.), petrels (*Fregetta* spp.), terns (*Sterna* spp.), and Bryde's whales (*Balaenoptera edeni*).

While weather influences were found to have minimal effects on gannet dive behaviours, higher winds were associated with lower altitude dives, and less frequent synchronous diving bouts. This is likely due to the decreased visibility of deeper prey caused by increased surface disturbances as a result of higher wind speeds, coupled with the inherent difficulties of performing highly coordinated aerial manoeuvres in high wind conditions.

Increased gannet flock sizes were found to correlate with more frequent high-altitude 90° dives, and increased rates of dive synchrony. This may be a result of the need to better coordinate dives in denser assemblages of con-specifics to avoid collisions, coupled with the increased foraging success associated with larger foraging groups, and local enhancement.

Increased foraging dolphin pods were also associated with more frequent high-altitude vertical dives. This may result from gannets capitalising on the increased bait-ball density and stability associated with larger foraging pods by taking deeper dives in order to make multiple prey captures with greater ease. Gannet synchrony,

however, was only found to decrease in the smallest dolphin pods, again attributed to the decreased foraging abilities of smaller pods.

Dolphin foraging behaviours most associated with the maintenance of dense stationary bait-balls were most heavily associated with high, vertical gannet dives, and increased gannet synchronous dives. This is likely the result of gannets capitalising on denser prey assemblages by taking deeper dives in pursuit of multiple prey capture.

The presence of Bryde's whales at MSFA's was found to decrease the frequency of both high vertical dives and synchronous dives, as lunge feeding on bait-balls scatters fish and decreases prey density.

The presence of hetero-specific avian species had various effects on gannet dive behaviours. Most notably, the presence of shearwaters and petrels was found to be associated with greater frequencies of low altitude gannet dives, thought to be a result of an increased collision risk in their presence. Terns meanwhile were associated with decreased dive synchrony, possibly as a result of false hetero-specific signalling caused by their white plumage.

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List of Abbreviations (in alphabetical order)

hrs.....hours

km/h.....kilometres per hour

Kw.....kilowatt

L..... litre

m.....meters

m/s..... meters per second

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1.0 Introduction

1.1 The Importance of Foraging

Foraging is a process in which an individual locates and exploits resources (water, nutrients, or energy) within its environment (Krebs, 1978). Foraging plays a key role in determining an individual's overall fitness, as it is an essential component of the ability to survive long enough to successfully reproduce (Krebs, 1978; Boggs, 1992). As an integral part of an individual's life history, the ability to forage effectively heavily influences the evolutionary development of a species' behavioural and biological adaptations. Individuals that display increased foraging success are more likely to propagate their beneficial genes to subsequent generations, improving the overall fitness of the species, and increasing the likelihood future generations will outcompete similar populations in the acquisition of limited resources (Pyke et al. 1977; Krebs, 1978; Boggs, 1992; Beckerman et al. 2010).

Over time, the selective pressures exerted by the challenges of successful foraging behaviour result in the tendencies of species to approach the "Optimal Foraging Model", wherein individuals within a species are able to obtain the highest ratio of energetic gains in relation to their energy expenditures (Pyke et al. 1977). This evolutionary drive towards foraging optimisation then provides the framework in which numerous aspects of a species ecology and life history can be studied, including physical and behavioural adaptations through the examination of energy flow, prey selection, and relative species fitness (Krebs, 1978).

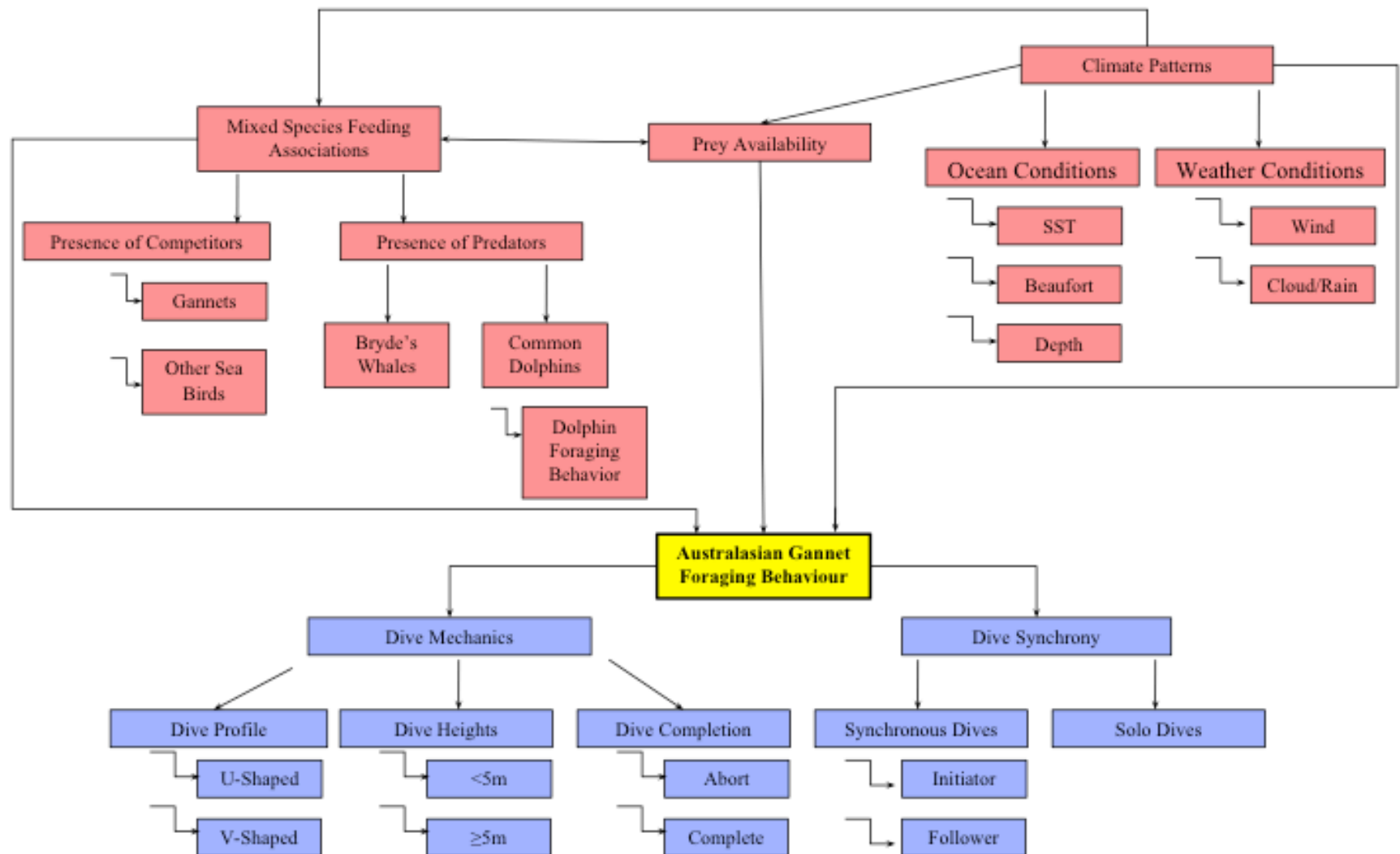


Figure 1. The relationships between foraging conditions and pressures (red) facing Australasian gannets (*Morus serrator*) and behavioural adaptations (blue) used to maintain an energetic surplus (modified from Benn, 2014).

1.2 Challenges of Foraging in a Marine Environment

Independent of habitat, the main challenges of foraging are common to all species. Individuals within a species must be able to locate and capture food sources in a timely enough manner to maintain an energetic surplus ample enough to sustain basic life functions (Norberg, 1977). Subsequently, foraging requires the proper management of time and energy budgets, however, endothermic, air-breathing, marine species must overcome additional physiological and environmental barriers associated with their unique habitat and physiology (Nagy, 1987; Costa et al. 2004; Rosen et al. 2007).

One of the primary challenges of foraging in a marine environment is that many pelagic prey species often travel in schools across vast distances, creating an environment of sparse and patchily distributed prey sources (Camphuysen & Webb, 1999; Makris et al. 2006). As a consequence, marine predators must have a highly developed strategy for locating sparsely available prey sources in a timely and efficient manner. Once a food source is located, the second challenge is the efficient capture of adequate prey. This is complicated in marine habitats, as prey must be captured in a physically demanding, three-dimensional environment. As such, air-breathing, homeostatic predators must not only have the ability to out manoeuvre and capture elusive prey, but must do so while mitigating the challenges posed by physiological constraints, including anaerobic dive limits, natural neutral buoyancy, and digestive constraints (Costa et al. 2004; Rosen et al. 2007).

In addition to the difficulties of energy acquisition, foraging in a marine environment is associated with an increased rate of energy depletion. Due to the

increased thermal conductivity of water and the harsh weather conditions associated with the marine environment, endothermic predators are under increased strain to account for the metabolic expenditures associated with maintaining proper thermoregulatory homeostasis (Nagy, 1987; Gremillet et al. 2001; Hamer et al. 2001; Lovvorn, 2007; Fort et al. 2011).

1.2.1 Challenges of Foraging Seabirds in a Marine Environment

Seabirds must not only overcome the unique set of foraging challenges associated with being an endothermic predator in the marine environment, but also the challenges posed by the unique biological requirements and the ecological constraints of being avian predators. Seabirds are central-place foragers, in that during the breeding season they rear their offspring at a nest that must be returned to between foraging trips (Orians & Pearson, 1979; Ropert-Coudert et al. 2004). The necessity to rear the chicks at the site of the nest means they must provide enough prey not only to meet their own energetic needs, but also those of dependent nestlings throughout breeding seasons (Nelson, 1966; Garthe et al. 1999; Ismar et al. 2010). The need to return to a central location further complicates seabird foraging ecology, as they are restricted to a “home range” in which all foraging must take place, further limiting the opportunities they may have to encounter prey (McNab, 1963; Schoener, 1968; Orians & Pearson, 1979; Ropert-Coudert et al. 2004). Furthermore, seabirds face additional foraging time constraints as the nest must be returned to in a timely manner between each foraging trip to ensure the chicks

remain fed and protected, and breeding partners are given a chance to forage themselves (McNab, 1963; Schoener, 1968; Orians & Pearson, 1979).

All these challenges must be overcome while compensating for the physical demands of hunting in two distinct environments (sea and air) (Thewissen & Nummela, 2008). This provides numerous foraging complications as seabirds must be able to travel, locate prey and navigate in an energetically efficient manner in one medium, while still being able to cope with the physiological pressures of underwater pursuit and capture. Prey capture is further complicated by their aerobic dive limits, which limit the depth at which pelagic prey can physically be pursued by individual birds (Schreer et al. 2001; Lovvorn, 2007), as well as their natural buoyancy levels, which dictate at what depths they must actively expend energy in the pursuit of prey (Lovvorn & Jones, 1991).

In order to meet these challenges, Australasian gannets (*Morus serrator*), a species in the family *Sulidae*, have developed numerous physical and behavioural adaptations that allow them to not only survive but form multi-generational colonies.

1.3 Australasian Gannets (Morus serrator)

Three geographically distinct gannet species make up the *Morus* genus: the Northern gannet (*M. bassanus*), native to the Northern Atlantic, the Cape gannet (*M. capensis*) which reside along the South African Coast, and the Australasian gannet (*M. serrator*) which is native to the coasts of Australia and New Zealand. The sexually monomorphic Australasian gannet (**Figure 2**) is the smallest and second

rarest species within the *Sulidae* family (Nelson, 1978). As the smallest of the three *Morus* species, Australasian gannets average between 84 and 91 cm in length, with a wingspan between 170-180 cm, and have an average approximate weight of 2.6kg (Nelson, 1978; Machovsky-Capuska et al. 2011b).



Figure 2. Photo of an Australasian gannet in the Hauraki Gulf, New Zealand.

(Photo: K. Hupman)

As central-place foragers, *Sulidae* species can serve as important ecological indicators; long-lived species favour adult survival, and will abandon current breeding efforts if there is sufficient environmental deterioration within their limited foraging range. While this has visible short-term effects on population dynamics, prolonged environmental conditions can result in the abandonment of long-term breeding colonies (Pichegru et al. 2010). Australasian gannets (hence

forth gannets) breed in dense coastal colonies in southeast Australia and New Zealand, and are the only gannet species found in New Zealand, with approximately 27 colonies located across both islands, 99% of which are located north of the 40°S latitude (Wodzicki et al. 1984; Burger et al. 1994). Average foraging distances from these colonies remains largely consistent when GPS trackers are used, with average maximum foraging distances between approximately 40–60 km from gannetries (Wingham, 1989; Machovsky-Capuska et al. 2013a, 2014).

1.3.1 Australasian Gannet Foraging Ecology

Gannets within New Zealand have been shown to have highly variable diets consisting of both coastal species, including pilchard (*Engraulis australis*) (Schuckard et al. 2012), as well as more oceanic species including saury (*Scomberesox saurus*), cubiceps (*Cubiceps caeruleus*) and kahawai (*Arripis trutta*) (Robertson, 1992; Bunce, 2001). Overall, more than 14 species have been identified as being targeted by gannets, 77% of which are between 11-20 cm in size (Wingham, 1985). While diets may vary between separate colonies (Wingham, 1985), gannet prey species are small, evasive, and can dive below a gannet's maximum foraging depths to avoid predation. Subsequently, prey capture can prove a difficult task, which gannets counter through the implementation of specialised dive techniques.

1.4 Plunge Diving Behaviour

“Plunge diving” is a behaviour in which a foraging bird spots a possible prey source from the air, before diving into the water at high-speeds for subsurface pursuit and capture. This foraging tactic provides access to pelagic prey otherwise inaccessible from the surface, and is utilised by a number of seabird species including terns (*Sterna* spp.) (Dunn, 1972; Taylor, 1983), tropicbirds (*Phaethon* spp.) (Le Corre, 1997), the Brown Pelican (*Pelecanus occidentalis*) (Carl, 1987), and Sulid species: boobies (Le Corre, 1997; Weimerskirch et al. 2005, Yoda et al. 2007) and gannets (Garthe et al. 2000; Ropert-Coudert et al. 2004; Machovsky-Capuska et al. 2011b; Wang et al. 2013).

Plummeting into the water is a highly specialised and complex foraging tactic. While Brown Pelicans have been recorded diving from heights of 18m (Carl, 1987), shearwater species (*Puffinus* spp.) have been found to initiate plunge dives from altitudes averaging 3-5m (Brown et al. 1978) and gannets have been known to initiate dives at heights in excess of 27m (though dives from 5-15m are more common) (M'Clymont, 1903; Oliver, 1955; Ellesat & Fricke, 2005). Gannets reach speeds of approximately 24m/s prior to impacting the water's surface (Ropert-Coudert et al. 2004; Wang et al. 2013). While dives generally only bring gannets to depths of 2 meters in search of prey, dives from height have been recorded to carry gannets as deep as 20.5m in New Zealand waters (Nelson, 1978; Green et al. 2010).

In order for gannets to effectively perform these aerial and subsequently sub surface manoeuvres, a number of morphological adaptations have

been developed in parallel with this behaviour. Among these are a specialised wing morphology and a streamlined body shape that reduces the aerodynamic costs of aerial locomotion (Brewer & Hertel, 2007), while also reducing drag and the energetic costs of pursuing submerged prey (Kooyman & Ponganis, 1998). In order to ameliorate the visual challenges associated with the sub surface light refraction experienced during underwater prey pursuit, gannets have developed a specialised light refractive optical lens (Machovsky-Capuska et al. 2012a). Additionally, an elaborate system of “inflatable” subcutaneous air diverticula tissues allow gannets to cushion the impact of high-speed water entry (Daoust et al. 2008; Wang et al. 2013). While gannet morphology plays an important role in enabling the performance of successful plunge dives, the behaviour itself is nuanced and highly evolved.

Plunge diving is an energetically expensive foraging tactic (Garthe et al. 2000; Weimerskirch et al. 2000; Lovvorn & Liggins, 2002; Green et al. 2010), and as such plunge divers must adapt to diving conditions in such a way as to ensure the rewards of prey capture outweigh the costs of the dive, a skill shown to take some species several years to master (Dunn, 1972; Carl, 1987; Zimmer et al. 2011). Dive variation in response to foraging cues is done in a number of ways by various species. For example, Cormorant species (*Phalacrocoracidae* spp.) foraging in benthic environments will increase underwater foraging times when diving at deeper depths in order to increase the odds of prey detection (Wilson & Wilson, 1988). Gentoo penguins (*Pygoscelis papua*) are known for taking shallower angle dives from the waters surface in order to assess prey density, and reserve more

energy to deeper dives for prey pursuit (Wilson et al. 1996). Common terns (*Sterna hirunda*) decrease dive heights in high winds to compensate for decreased visibility of deeper prey (Taylor, 1983). Gannets have also been shown to use a number of dive variations under varying conditions, including shallow surface dives, plunge dives, and pursuit plunging, in response to the depth and density of prey populations (Ropert-Coudert et al. 2004, 2009; Machovsky-Capuska et al. 2011b; Machovsky-Capuska, 2012b).

The two most commonly utilised dive variations are the “U-shaped” and “V-shaped” dive profiles. V-shaped dives are characteristically shallow, of shorter duration, and rely primarily on the dives' momentum to ensure prey capture, while U-shaped dives are more vertical in nature, carry the gannets to deeper depths, and rely on a subsequent active pursuit phase for individual prey pursuit and capture (**Figure 3**; see Garthe et al. 2000; Machovsky-Capuska et al. 2011b; Machovsky-Capuska, 2012b).

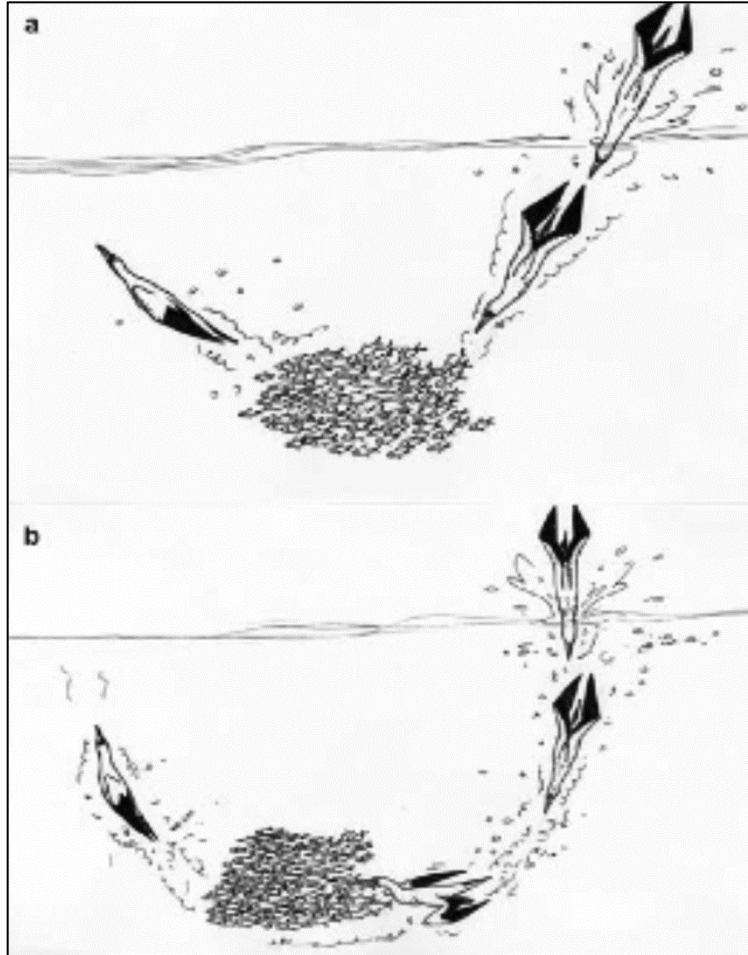


Figure 3.
Variations in
gannet dive
profiles:

a) The
characteristics of a
“V-shaped” dive.

b) The
characteristics of a
“U-shaped” dive.

Drawing not to
scale.

(From Machovsky-
Capuska et al.
2011b.)

It has been demonstrated in Machovsky-Capuska et al. (2011b), that each dive type carries with it different energetic tradeoffs. Where V-shaped dives are shorter in duration, and less energy intensive than U-shaped dives, they yield fewer captured prey, and are less likely to result in prey capture than their U-shaped counterpart. When prey capture success is accounted for however, the relative tradeoffs associated with each dive type has been proven to have comparable energetic efficiencies per unit time spent carrying out each respective profile (Machovsky-Capuska et al. 2011b). How gannets determine which dive profile to carry out is still an area of ongoing debate and research.

One theory suggests that, like gentoo penguins, shallow V-shaped dives may be reserved for assessing prey density (Machovsky-Capuska, 2012b). Earlier studies hypothesised that dive profiles varied in response to different sized prey, with V-shaped dives preferred in the pursuit of larger fish (Garthe et al. 2000), while subsequent studies have advanced the theory that dive variations may instead depend on the species of prey (Elliot et al. 2008). More recent studies proposed that the depth of the prey rather than its size or species is the leading factor influencing dive variations (Machovsky-Capuska et al. 2013b). Dive variations may also depend heavily on the influence of external variables, including weather conditions and the competitive influence of con-specific and hetero-specific foragers. While numerous studies conducted on gannet foraging behaviours have shown they are highly capable aerial predators, few studies have been conducted on the mechanisms of gannet dive behaviour at the foraging sites themselves (Ellesat & Fricke, 2005; Machovsky-Capuska et al. 2011b, Machovsky-Capuska, 2012b, Machovsky-Capuska et al. 2013b).

1.5 Common Dolphins (Delphinus sp.)

The common dolphin (*Delphinus* sp.) is a small-toothed member of the Delphinidae family, with adult males varying in size between 1.7 and 2.3 meters in length and weighing between 70 and 200 kg (Shirihai, 2006). They are most easily identified by the distinctive tan to ochre, tri-coloured hourglass marking that runs the length of their bodies, an uncharacteristically ornate colouration for a Delphinid (Mitchell, 1970; Shirihai, 2006).

Common dolphins occur around much of New Zealand's coastline, which forms the southern limit of their population range (Stockin et al. 2014). With the exception of a year round population established in the Hauraki Gulf, dolphin occurrence around the country is largely seasonal, and most generally concentrated around the North Island (Gaskin, 1968; Stockin et al. 2008a, 2014). Seasonal shifts in common dolphin abundance within the north-western Bay of Plenty have been linked to sea surface temperatures (SST), wherein the distribution of dolphins has shifted further out to sea in winter months (Neumann, 2001).

Around New Zealand's North Island, a study of common dolphin stomach contents revealed a total of 31 fish and seven cephalopod species made up the diet (Meynier et al. 2008b; Stockin 2008a). Of these species, the most commonly identified prey was arrow squid (*Nototodarus* spp.), jack mackerel (*Trachurus* spp.), and anchovy (*Engraulis australis*), with the majority of prey being small pelagic fish, in keeping with the findings of other studies around the world (Young & Cockcroft, 1994; Pusineri et al. 2007; Meynier et al. 2008a; Spitz et al. 2010).

1.5.1 Common Dolphin Foraging Behaviour

In order to successfully forage for such a varied and diverse number of prey species in both pelagic and neritic environments, common dolphins display a number of different foraging tactics, and a wide range of behaviours, both individually and coordinated within a group. These foraging manoeuvres include a number of distinct variations examined in Neumann & Orams, 2003. Individual foraging behaviours observed in common dolphin foraging include "high-speed pursuits",

“kerplunking”, and “fish whacking” (Neumann & Orams, 2003). High-speed pursuits involve the individual pursuit of prey across the water's surface for capture. Kerplunking manoeuvres occur when dolphins slam their tail flukes against the water's surface, creating a percussive sound. Finally, fish whacking manoeuvres involve the striking of individual prey with the tail flukes, stunning them and allowing for easy capture.

Common dolphin's foraging behaviour relies on group behaviours wherein coordinated herding manoeuvres are used to manipulate prey into more easily managed aggregations (Würsig, 1986; Neumann & Orams, 2003; Burgess, 2006).

The foraging strategies observed in common dolphins include “line-abreast” formations, in which a foraging group of dolphins cooperatively drives prey ahead of them (**Figure 4**), “wall formations”, in which a line of dolphins drives fish towards another group of dolphins, “carouselling” (**Figure 5**), “bubble blowing” in which dolphins startle groups of fish by releasing bubbles of air below them, and “synchronous diving” in which many members of a foraging group dive together and resurface in synchrony under fish schools (Neumann & Orams 2003; Burgess, 2006).

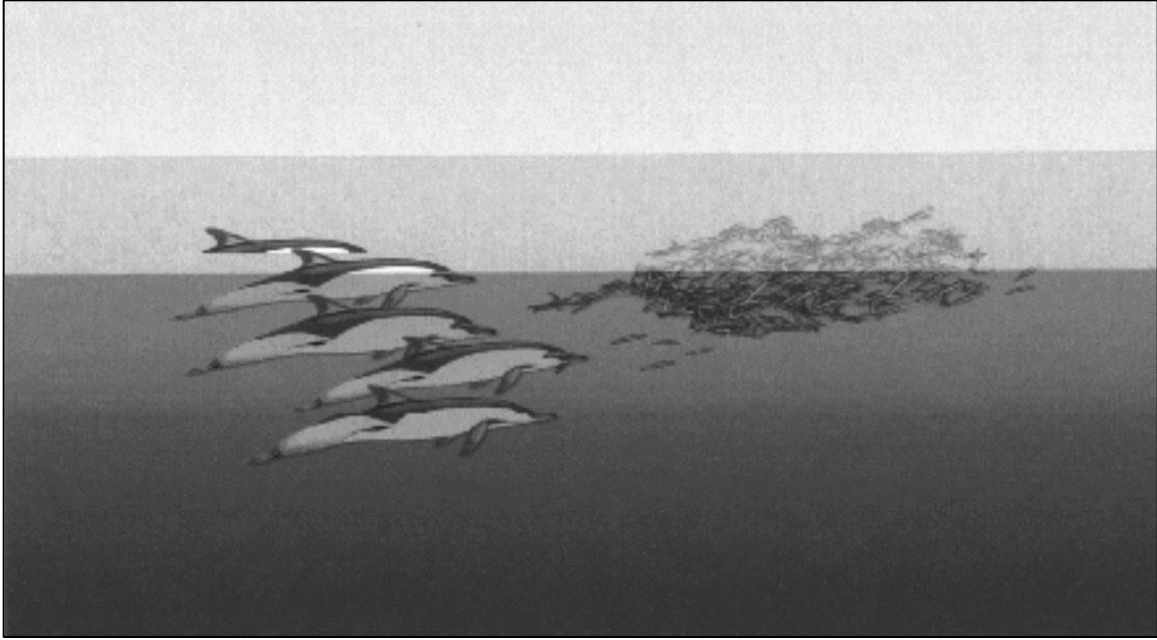


Figure 4. Line-abreast: Dolphins swim side-by-side, driving fish before them (Neumann & Orams, 2003).

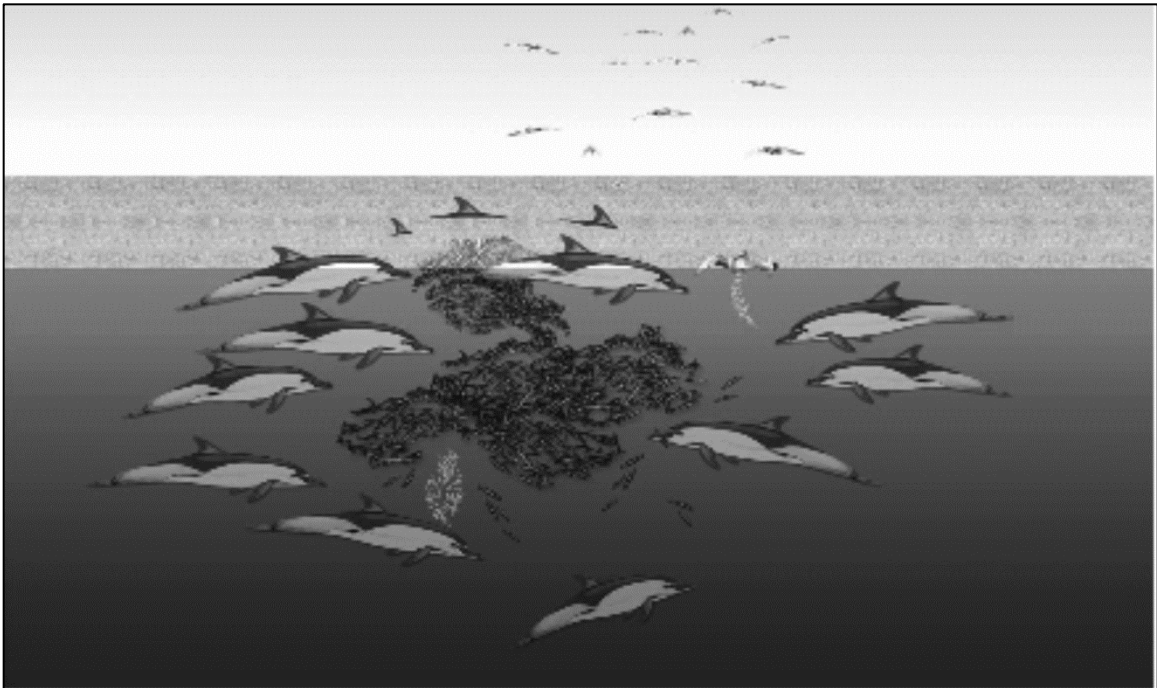


Figure 5. Carouselling: Dolphins cooperatively encircle a school of prey, trapping them in a "bait-ball" against the surface (Neumann & Orams, 2003).

Within the Hauraki Gulf, the most prevalent behaviour observed of foraging dolphins was the synchronous diving, occurring in over 80% of observed foraging groups (Burgess, 2006). The implementation of various herding tactics was also shown to vary from congregation to congregation, as well as within a single foraging event, with dolphins using a variety of manoeuvres within a single chase (Burgess, 2006).

These feeding congregations and herding manoeuvres, are often so effective at corralling pelagic prey into tight easily accessible balls at the water's surface (referred to as "bait-balls") that other aquatic species will often congregate to feed on them as well, taking advantage of the common dolphin's foraging behaviour to grab an otherwise inaccessible or difficult meal (covered in detail in section 1.7).

1.6 Bryde's Whale (Balaenoptera edeni)

Balaenopterid species are medium sized rorqual whales with a worldwide distribution. While the actual number of Balaenopterid species remains uncertain, the species most frequently observed in New Zealand coastal waters are Bryde's whales, *Balaenoptera edeni* (Wiseman et al. 2011). Physically mature Bryde's whales average between 11m and 12m in length, (Junge, 1950; Rice, 1977) and feed primarily on small fish, including anchovy and pilchard, cephalopods and plankton (Tamura et al. 2009; Wiseman, 2008). Although Bryde's whales are largely solitary, they are known to feed in conjunction with other marine species with relative frequency (Ellesat & Fricke, 2005; Stockin et al. 2009). Some studies indicate that as

many as 70% of common dolphin feeding events observed in the Hauraki gulf involve Bryde's whales (Stockin et al. 2009). During such feeding opportunities Bryde's whales will often capitalise on the work of common dolphins by lunge feeding on condensed bait-balls, often times temporarily scattering MSFA's or bringing them to an end (Wiseman, 2008).

1.7 Mixed Species Feeding Associations (MSFA's)

In accordance with the niche partitioning theory, wherein species with similar ecological requirements compete for resources, competing species' co-existence will require at least some degree of resource (prey or habitat) partitioning (Pianka, 1974). While partial resource partitioning may be achieved through the exploitation of different microhabitats, including the preference of different prey species, prey sizes or different temporal foraging preferences, sympatric species may also jointly exploit resources through the formation of "mixed-species" associations (Bearzi, 2005; Qu  rouil et al. 2008; Zaeschmar et al. 2013). Mixed-species associations are temporary aggregations of individuals of different species involved in similar activities for time periods ranging from several minutes to hours, days, or even years (Stensland et al. 2003; Qu  rouil et al. 2008). These associations are most commonly observed in birds (Sridhar et al. 2009) and primates (Chapman & Chapman, 2000). However, as socially dependent animals foraging in marine environments, with often patchily distributed prey sources, there are numerous examples of MSFA's forming in conjunction with common dolphins and other cetacea. Included in these are examples of hetero-specific foraging associations

between different delphinids in the Bahamas (Herzing et al. 2003) and the Mediterranean (Forcada et al. 1994; Frantzis & Herzing, 2002), the Pacific Ocean, (Psarakos et al. 2003) and around New Zealand (Zaeschar et al. 2014), as well as between delphinids and fish species like albacore tuna (*Thunnus alalunga*) (Das et al. 2000; Clua & Grosvalet, 2001), and numerous avian species (Evans, 1982).

While there are thought to be multiple social and reproductive advantages to the formation of these aggregations, it is hypothesised that there are two primary reasons mixed-species associations are formed (Stensland et al. 2003). The first of these, the predator avoidance hypothesis, postulates individuals may benefit from associations through the increased likelihood of predator detection by other group members, as well as from the risk dilution of predation associated with a group. The second, the foraging advantage hypothesis, theorises that individuals benefit from the association by summing up their capacities to detect and exploit patchily distributed food resources (Clark & Mangel, 1986; Bednekoff & Lima 1998; Quérrouil et al. 2008). These two hypotheses are not mutually exclusive, and in some taxa, individuals in mixed-species groups increase their capacities for predator detection as well as their foraging efficiency (Sullivan, 1984; Gautier-Hion et al. 1983; Chapman & Chapman, 2000). It is also important to note that multi-species associations may not be equally beneficial to all the species involved, and some species may act as social parasites to another, or even exhibit Kleptoparasitic behaviours to others foraging within the group (Quérrouil et al. 2008; Machovsky-Capuska et al. 2012b).

It has been theorised that seabird species foraging on unpredictable prey sources may use the behavioural cues of other animals in order to maximise their foraging success in a process known as “Local Enhancement” (Machovsky-Capuska et al. 2014; Thiebault et al. 2014). The mechanisms to detect cues for prey availability may include the observation of con-specifics (Silverman et al. 2004; Thiebault et al. 2014) and oceanographic features (Schneider, 1982). The interactions with con-specifics in particular are thought to play a major role, especially when animals congregate in high densities (Buckley 1997; Machovsky-Capuska et al. 2014; Thiebault et al. 2014; Tremblay et al. 2014).

Notable among seabird species that form associations with Delphinids are gannets, which are also known members of numerous MSFA’s around the world. While plunge-diving behaviour is exhibited by individual foraging gannets, they will often forage in small groups of two to six individuals, but have been recorded in larger groups, having more than 500 individuals in a flock, with the formation of larger flocks being associated with the presence of foraging con-specific cetacean species and predatory fish (Ellesat & Fricke, 2005).

Gannets have been observed to forage in association with harbour porpoises (*Phocoena phocoena*), the white-beaked dolphin (*Lagenorhynchus albirostris*), dusky dolphin (*L. obscurus*) (Vaughn et al. 2007), common dolphin, and Bryde’s whale (Ellesat & Fricke, 2005; Stockin et al. 2008a; 2009; Wiseman, 2008) among other species, including numerous associated bird species (Camphuysen & Webb, 1999). Gannets may be one of the main beneficiaries of these foraging congregations, as Delphinids often corral fish to the surface during foraging, eliminating the problems

posed by a limited diving depth in pursuit of prey for plunging seabirds (Evans, 1982; Au & Pitman, 1986; Ballance & Pitman, 1999; Camphuysen & Webb, 1999).

Likewise, common dolphins are also well known members of MSFA's. They have been observed in sympatric associations with a number of other cetacean species (Forcada et al. 1994; Frantzis & Herzing, 2002; Bearzi, 2005; Stockin & Orams, 2009), and are frequently observed in association with a great number of seabird species, including shearwaters (*Puffinus* spp.), boobies, terns, gulls (*Larus* spp.), petrels (*Fregetta* spp.) kittiwakes (*Rissa tridactyla*) and gannets. (Evans, 1982; Au & Pitman, 1986; Ballance & Pitman, 1999; Clua & Grosvalet, 2001).

Within New Zealand waters, the largest congregations of foraging gannets have been observed to form in association with common dolphins, Bryde's whales and predatory fishes like kahawai and kingfish (*Seriola lalandi*), and are most commonly joined by other seabirds, including flesh-footed shearwaters (*Puffinus carneipes*), Buller's shearwaters (*P. bulleri*) and fluttering shearwaters (*P. gavia*). These associations are based on the exploitation of the same prey species and are indicative of inter-specific foraging cooperation (Ellesat & Fricke, 2005).

1.8 Synchronous diving

While foraging in mixed species feeding events provides gannets with increased access to prey, navigating and hunting in high-density assemblages of con-specific and hetero-specific predators also poses additional challenges that must be overcome. The increased number of foraging individuals feeding on limited prey sources increases the amount of foraging competition within the feeding

aggregation (Camphuysen & Webb, 1999; Couzin & Krause, 2003). Along with the additional competition for prey, the occurrence of kleptoparasitism, in which prey is poached from an individual that has successfully completed prey capture by others foraging within the group, increases accordingly (Brockmann et al. 1979; Garthe & Hüppop, 1998).

In order to minimise the strains of excessive competition for resources on a prey source that is finite, social foraging species often develop a specialised structural order, wherein individuals within the group are able to communicate or draw behavioural cues from others within the group (Krebs et al. 1972; Brockmann & Barnard, 1979; Couzin et al. 2002). This is a particularly important practice for gannets, as they are also exposed to the risk of being involved in high-speed aerial collisions. While plunge diving for prey has been shown to be a highly successful behaviour in enabling adequate prey capture, the manoeuvre, complicated by increased predator density, has also been implicated in multiple fatalities, in which a diving bird can incidentally strike and kill gannets that have plunged previously (Machovsky-Capuska et al. 2011a).

In order to alleviate the risks and associated drawbacks of foraging in tightly packed feeding congregations while maximising prey capture success, gannets coordinate dives via the behaviour of dive-synchrony. When following a shoal, the birds at the front edge of a group dive whilst behind them, previous divers emerge on the surface, rest on the water or take off to fly forwards and rejoin the diving birds (Nelson, 1978). At the head of the flock, a diving gannet will initiate a dive, likely as a response to locating prey, and on occasion will be closely followed by

other diving gannets (Machovsky-Capuska et al. 2012b). Whether these synchronous dive events are an example of local enhancement, wherein individuals respond to common cues, such as a direct prey sighting, or to previously diving birds, is currently unknown. Additionally, the dynamics of these synchronous diving events are poorly understood in relation to the MSFA as a whole. Whether the behaviour of con-specifics plays a role in their formation remains unknown.

2.0 Aims

2.1 Plunge Diving

Plunge diving behaviour is integral to gannets' ability to successfully capture prey while feeding in MSFA's. The mechanics governing this behaviour however, are not fully understood. This project aims to examine how variations in plunge diving behaviour are used in order to maximise foraging success. Specifically, I will test the hypothesis that 90° dives are primarily initiated from heights exceeding 5m. Additionally, it is hypothesised that 90° dives taken from height will decrease in frequency when foraging occurs in high winds, or under harsh oceanographic conditions.

2.2 MSFA's

Foraging in tight rapidly changing congregations of hetero-specifics is of vital importance to gannet foraging ecology. Foremost among the species influencing these aggregations are common dolphins, which directly influence the location and

density of pelagic fish species while foraging. This thesis also aims to determine what influences the presence of other foraging species have on gannet plunge diving behaviour, in addition to determining the potential influence of common dolphin herding behaviour on gannet dives. Specifically, I aim to test the hypothesis put forth in Machovsky-Capuska et al. (2012b), which suggests foraging common dolphins will indirectly influence gannet dive behaviour; hypothesising V-shaped gannet dive profiles will be more prevalent in the presence of common dolphins, as fish are readily corralled to the surface. Additionally, I aim to determine what, if any, common dolphin foraging cues may act as gannet dive initiator cues. As common dolphins employ numerous and distinctive coordinated group-foraging manoeuvres (outlined in Neumann & Orams, 2003), it is likely that gannets will attempt to maximise prey capture success by initiating dives in response to specific dolphin cues. It is hypothesised that the highest percentage of dive initiations will occur in response to dolphin “carouselling” behaviour, as fish are kept stationary and densely packed at the water’s surface, while dolphins remain visible, and located outside of the main bait-ball concentration. No data yet exists to support the hypothesis that gannets adapt plunge diving behaviour in direct response to common dolphin foraging behaviour.

Finally, the impact of foraging Bryde’s whales and con-specific seabirds on gannet behaviour will be further assessed. It is hypothesised Bryde’s whale presence will be associated with decreased gannet synchronous diving behaviour, as other hetero-specifics are likely to scatter on their approach, dispersing concentrated bait-balls. The presence of con-specific seabirds is thought to

decrease the number of gannet dives, as well as lowering gannet dive altitudes, as increased competition will decrease prey availability, and increased surface predator presence will hinder diving ability.

2.3 Dive Synchrony

The parameters influencing gannet plunge dive synchrony events are still not fully understood. Whether it is used as a form of local enhancement on the basis of prey location or hetero-specific behaviour remains unknown. This thesis aims to determine what hetero- or con-specific cues are associated with synchronous dive behaviour. It is hypothesised that longer synchronous dive events may be correlated with increased numbers of foraging dolphins and gannets, as increased dolphin foraging behaviour will be likely to provide more densely packed bait-balls, while synchronous diving events become essential in avoiding collisions with increased hetero-specific presence.

3.0 Methods And Materials

3.1 Study Site

The study took place within New Zealand's Hauraki Gulf, a shallow, semi-enclosed body of water on the northeast coast of North Island, New Zealand (**Figure 6**). It is bordered to the southwest by the mainland, to the east by the Coromandel Peninsula and in the north by several islands. The three main channels: Jellicoe (between the mainland and Little Barrier Island), Colville (between Great Barrier

Island and Coromandel) and Craddock (between Little and Great Barrier Island) form a connection to the Pacific Ocean. Specifically, the study covered the inner area of the gulf, between Takatu Point and Kaiti on the tip of the Coromandel peninsula.

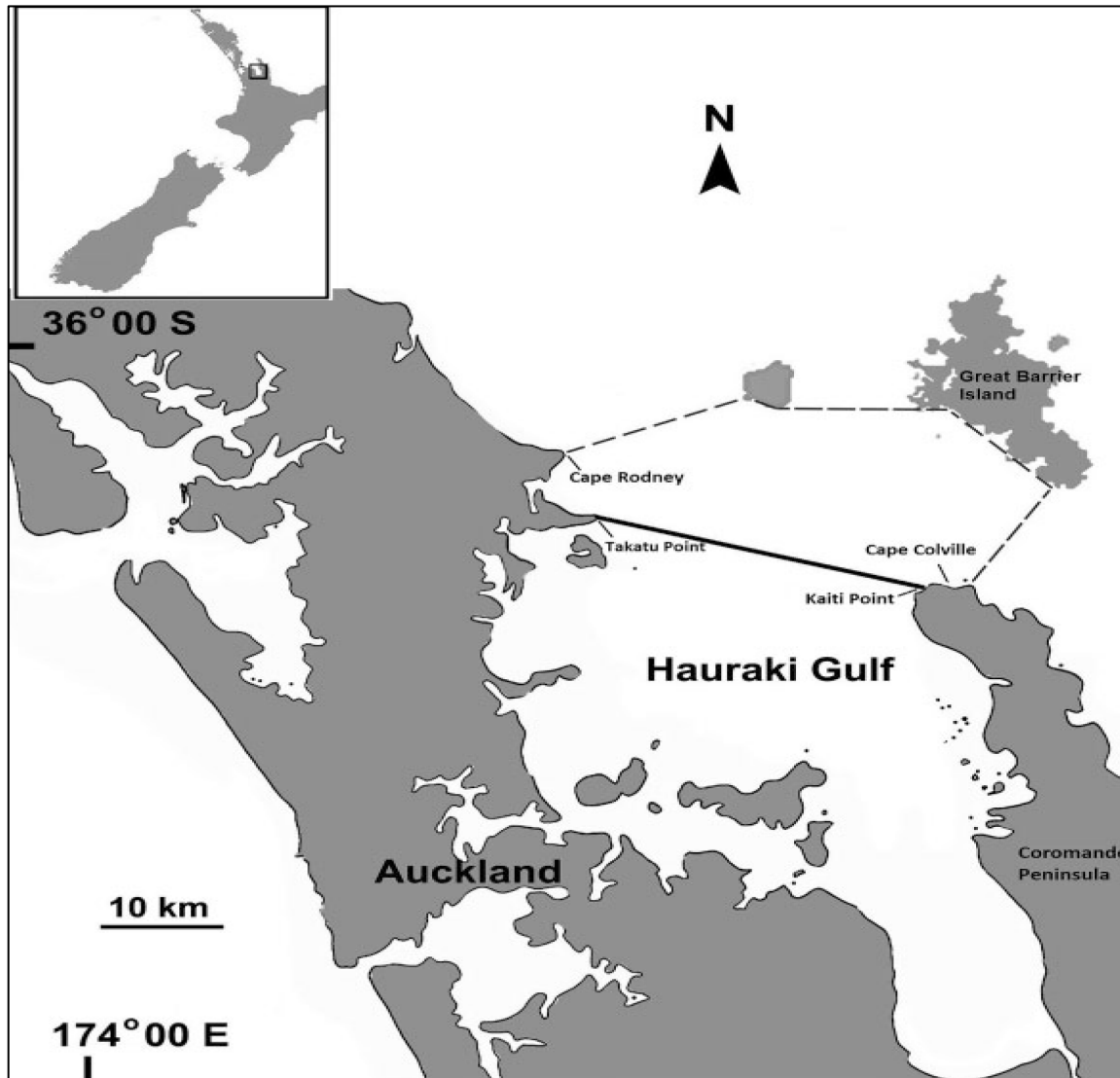


Figure 6. A map of the study location and geography of the Hauraki Gulf, New Zealand. The Inner Gulf is marked by the dark line, while the broken lines delineate the outer gulf (Source: Hupman et al. 2014).

3.2 Data Collection

3.2.1 Research Vessel

Surveys took place from March 2013 and June 2014 (excluding December 2013) aboard *Dolphin Explorer* (**Figure 7**), a commercial whale-watching vessel that supports marine research in the gulf. *Dolphin Explorer* is a 20m catamaran with two 300 kW Scania 9 L diesel engines, and a cruise speed of 17 knots with a maximum capacity of 100 passengers. Cruises are conducted daily, with harbour departure times of 11:30 in the winter and 13:30 in spring and summer months, and are approximately six hours in duration. Trips are dependent on weather conditions, with winds in excess of 25 knots, heavy precipitation or a Beaufort >4 resulting in trip cancellations.



Figure 7. *Dolphin Explorer*

(www.corporatexplore.co.nz/images/04_AWD.jpg)

Three observers continuously scanned the horizon using hand-held binoculars (Pentax 8X40) for signs of bird and marine animal activity. This included: splashes (i.e. dolphin jumping), marine mammal blows, dorsal fins or aggregations of seabird species.

3.2.2 Approach and Data Collection

Departure time and date information was recorded upon the start of each trip. Upon encountering a MSFA event or group of marine mammals, *Dolphin Explorer* would slowly approach to a distance of approximately 300m and stop to assess behaviour and course in order to minimise potential negative effects on the observed animals (Mann et al. 2000). Subsequently, the vessel would approach the rear of the aggregation at a low and constant speed approximately 100m from the event. During this time environmental and MSFA parameters were recorded. Weather parameters (cloud cover, wind speed, visibility and Beaufort sea scale), sighting times and durations, sea surface temperature (SST) and GPS coordinates of the sighting location, along with any relevant notes about the associated species was recorded. This data was used to aid in determining what environmental parameters were influencing the behaviours of species within the MSFA.

The number of gannets, common dolphins, and Bryde's whales were estimated by the primary observer upon approach, and re-examined and altered accordingly upon video review. The number of foraging individuals of each species

was recorded as “minimum”, “maximum”, and “best estimate” (as per Dwyer et al. 2014) for all individuals in an aggregation. Aggregations were defined as containing any number of individuals appearing to be in association, regardless of foraging, socialising or travelling states.

If the followed aggregation contained foraging gannets, they were filmed by the primary observer, using a Canon XH A1S high definition video camera. The video camera features 20 mm zoom and films at 30 frames per second frame rate. All video was shot from the upper deck of *Dolphin Explorer*, at 5m above the waters surface to maintain consistent height and angles across film collection. The horizon was used as a frame of reference to ensure gannet dive heights and angles could be measured consistently. The camera zoom varied between and within feeding events to allow for maximum data collection. The best estimate of dolphin and gannet numbers was confirmed or amended upon video review. The film was subsequently analysed to determine gannet initiation factors, as well as water entry dive angles, dive heights, dive frequencies, and environmental influences effecting dive mechanics (see 3.3 Data Analysis).

3.3 Data Analysis

3.3.1 Gannet Dive Mechanics

Each gannet dive and their subsequent entry into the water (assuming dive completion) was reviewed frame-by-frame using Avidemux v2.6 video-editing software, and recorded in Excel v12.3.6 using the corresponding video frame time-signatures (to the hundredth of a second) wherein the event took place. Gannet dive

mechanics were completed in accordance with Machovsky-Capuska, 2012b (chapter 5) wherein a gannet was deemed to have initiated a dive at the moment it's wings spread fully and it began to rotate it's body, or drastically lowered it's body in relation to the water, and was deemed to complete a dive at the moment it became fully submerged (**Figure 8**).

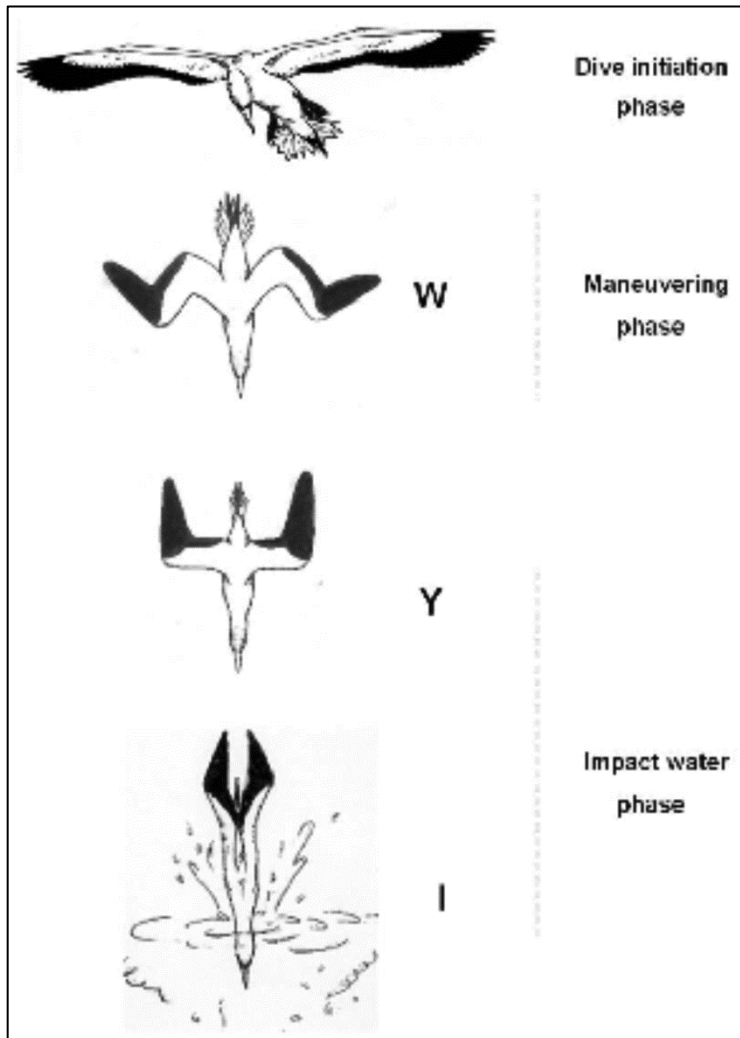


Figure 8. Stages of a gannet dive used to determine dive behaviour (Source: Machovsky-Capuska 2012b).

If a dive was initiated, but subsequently aborted before completion, the individuals' time slot for completion time was marked as "aborted", in order to gain

an understanding of factors influencing dive completion frequencies. Any gannet dives that were only partially captured (including only an initiation or completion) were recorded as only containing the captured portion of the dive.

The angle of entry of each gannets completed dive was also recorded as either 45° or 90°. This was done using the protocol adapted from Machovsky-Capuska et al. (2013b), in which the angle of water entry was only measured for dives that occurred in the plane perpendicular to the cameras optical axis, using the waters surface as a horizontal reference plain. That is to say, data was only collected from dives that occurred perpendicular to the cameras line of sight, all other dives were excluded from the analysis. Analysed frame-by-frame using Avidemux v2.6, 45° dives were deemed to be any dive in which the gannets body was approximately 50° or less, in relation to the waters surface, while 90° dives were classified as any dive in which the gannets body was greater than 70° or vertical to the waters surface, upon entrance. Any dives occurring within 10° either side of an angle 60° perpendicular to the waters surface were excluded. Any dives completed that could not satisfactorily be identified as fitting either trajectory, due to their distance from the filming platform, or other visual obstructions were excluded from the data set.

Dive heights were determined using the filming platform (the ships top deck) as an altitude reference, wherein dive initiations were deemed to take place above or below the filming researcher, and grouped into two categories as occurring either <5 meters or ≥ 5 meters above the water. Gannet dives in which the initiation time was not recorded were excluded from the data.

In order to compensate for any overstated standard error in the data analysis caused by the large sample of gannet dives, gannet dives were sorted into two nested categories. The larger, “Feeding Event” differentiated one MSFA from another, with all recorded foraging behaviour taking place within a feeding event being carried out by the same congregation of animals. The smaller category “Work Up” was recorded as containing gannet feeding activity confined to a distinct spatial and temporal region of high feeding activity within the feeding event. Gannet diving mechanics were analysed using R studios statistical software v0.98. Possible correlations between the different aspects of gannet diving mechanics (height, angle, completion) were examined using General Estimating Equations (GEE’s; “geepack” R Package) (Liang & Zeger, 1986; Pickles, 1998; Halekoh et al. 2006; Braaker et al. 2014). All GEE’s were nested using the Feeding Event and Work Up categories in order to account for the inherent correlation between gannet behaviours in the same groups by including an additional variance component for correlation structure within MSFA data clusters. GEEs are highly recommended if the focus is on a population's averaged response (Fieberg et al. 2009; Koper & Manseau, 2009).

3.3.2 External Influences on Gannet Diving Behaviour

Each individually recorded gannet plunge dive, and their corresponding diving mechanics were grouped with weather and MSFA composition data corresponding to the time the plunge dive took place. Weather parameters included wind speed grouped into three categories (<10km/h, 11-27km/h and >28km/h), sea state

(following the Beaufort scale) and cloud cover (none, partial, overcast, raining). Depth (to the closest tenth of a meter), and SST (to the closest tenth of a degree Celsius) were also recorded alongside each feeding event using *Dolphin Explorer's* on board depth finder and SST reader, respectively. Results for depth and SST are later presented as mean and SE.

Additionally each plunge dive was paired to the data recorded on the MSFA's composition, including the presence/absence of shearwater species, petrel species, terns (*Sterna striata*), Bryde's whales and the number of foraging gannets and common dolphins within the MSFA feeding event. Gannet and dolphin numbers were separately grouped into nine categories as (0, 1-10, 11-20, 21-50, 51-100, 101-200, 201-500, 501-1000 and 1001+). In order to create groups with a comparable number of recorded occurrences, these were later condensed into the categories (1-100, 101-500 and 500+) for gannets and (0, 1-100, 101-500 and 501+) for dolphins. In order to determine whether a given temporal parameter or con-specific presence had a significant influence on gannet plunge diving mechanics, while controlling for unknown correlations, each recorded category was tested against gannet diving parameters for significance using a GEE Statistical Test.

Recorded dolphin foraging behaviours included carouselling, line-abreast and synchronous dives, as outlined in Neumann & Orams (2003). Each of these was tested against gannet dive variations using the same methods.

3.3.3 Synchronised Plunge Diving

Gannets synchronise their dives within spatial and temporal criteria (Machovsky-Capuska 2012b). In order to determine what mechanisms influence the formation of synchronous diving events in gannets, dives were labelled in three different categories following Machovsky-Capuska (2012b): i) an “*Initiator*” was the first gannet, within a flock, that rotated its body or decreased its height in respect to the water exhibiting an intention to plunge dive; ii) a “*Follower*” was any con-specific that dove within the time that the first bird initiated its dive and entered the water (e.g. synchronisation time) and within 10m of the initiation’s plunge dive; iii) a “*Solo Dive*” occurred when no bird followed the Initiator’s plunge dive within the synchronisation time. Initiators and Followers together made up “synchronous diving bouts” (a.k.a “synchrony”), while Solo divers were not included in synchronous data.

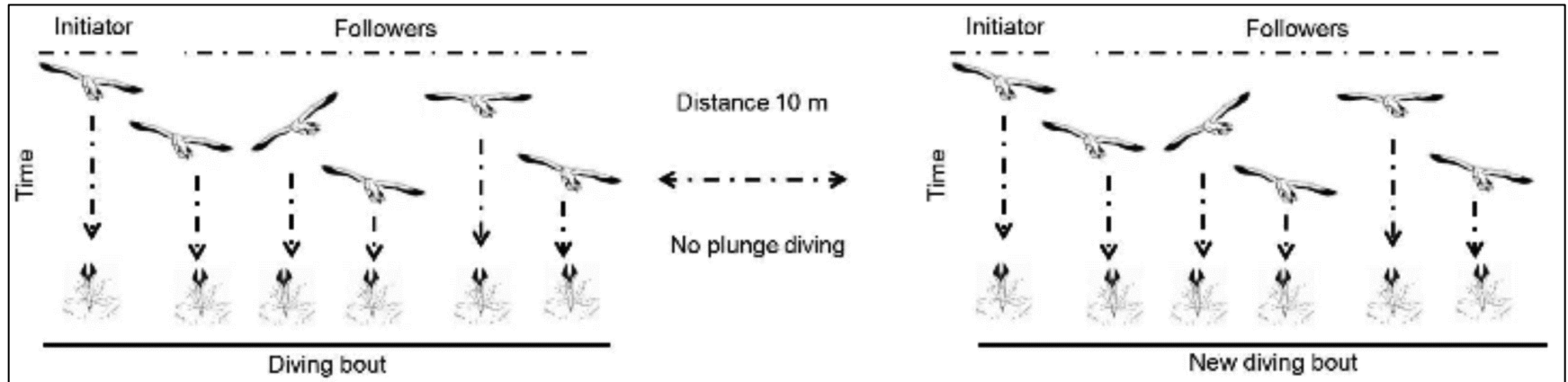


Figure 9. Synchronised plunge-diving in different diving bouts of gannets (Source: Machovsky-Capuska 2012b).

In order to determine the effect of external influences on the formation of synchronous diving bouts, the rate ratio of Initiator and Follower dives were run against a number of parameters using GEE models to determine the degree of influence different parameters have on synchronous diving bout formations. Again GEE analysis was used to account for the inherent influences of gannets diving within the same Work Ups and as such nested data, including an additional variance component for correlation structure within MSFA data clusters was used. The effect a given independent variable (cons- and hetero-specific presence and abundance, weather conditions) had on dive synchrony was determined by examining the relative change in Initiator and Follower dive frequencies per unit time when compared to the different degrees of independent variables. Increases in the rates of Initiator dives were indicative of highly numerous synchronous diving bout formations whereas an increase of Follower frequencies was indicative of increasing diving bout size and duration.

Additionally, in order to determine whether a given temporal parameter or con-specific presence had a significant influence on variations in overall synchrony percentages, each recorded category was tested against gannet diving synchrony, using a cross tabulations and GEE statistical test.

4.0 Results

4.1 Field Effort

Data was collected between March 2013 and June 2014 (excluding December 2013). Forty-five independent boat-based surveys were conducted aboard *Dolphin Explorer*, culminating in the collection of approximately 11.9hrs of MSFA video footage. High quality video footage from MSFA events occurred during 51.1% of survey trips (n = 23), resulting in a total of 5565 recorded gannet plunge dives.

4.2 Diving Mechanics

From a total of 4466 recorded dives containing both an initiation height and angle of entry into the water, the majority 69.0% (n=3083) were initiated $\geq 5\text{m}$ and completed at 90°s (**Figure 10**).

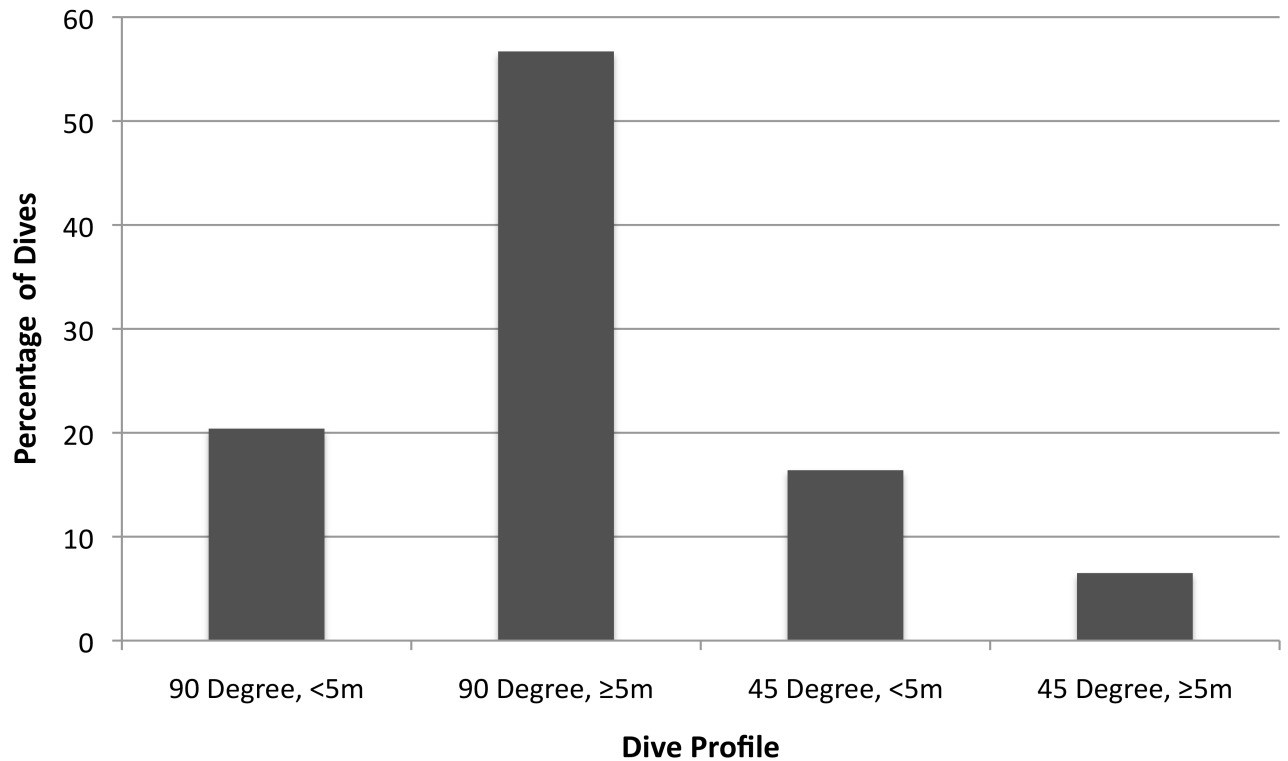


Figure 10. The total ratio of dive profiles recorded in foraging gannets in the Hauraki Gulf, New Zealand.

4.2.1 Dive Completions

An examination of diving rates based on the total number of gannets observed to exhibit a dive initiation behaviour (n=5440), showed that completion occurred in 94.7% of cases (n=5153), while dive abortions occurred in only 5.3% of recorded dives (n=287).

4.2.2 Diving Altitude

Of the 5100 dives recorded indicating a dive initiation height, 74.6% (n=3804) were initiated at an altitude $\geq 5\text{m}$, while the remaining 25.4% (n=1296) were initiated $< 5\text{m}$.

Out of 1270 dives initiated $< 5\text{m}$ above the water, 95.9% (n=1218) were carried out to completion. Likewise, out of 3,712 dives initiated $\geq 5\text{m}$ above the water, 93.7% (n=3480) were carried out to completion (GEE: Wald test, $z = 5.15$, $SE = 0.252$, $P < 0.05$). These results suggest that diving altitude has little effect on successful completion.

4.2.3 Diving Angle

Of the recorded 4878 dives that decisively show an angle of entry, 85.4% (n=4164) were found to be 90° 's in nature, while the remaining 14.6% (n=714) occurred closer to the 45° angle.

4.3 Gannet Flock Size Influence on Dive Mechanics

The size of the foraging gannet flock had a significant influence on dive angles, wherein the percentage of 90° dives increased with flock size from 77.8% (n=818) of the total dives in flocks with less than 100 gannets (n=1052), to 86.1% (n=1967) of total dives in flocks with 101-500 gannets (n=2285) and 89.5% (n=1379) in the largest flocks of 501+ birds (n=1541) (GEE: Wald test, $z = 7.26$, $SE = 0.197$, $P < 0.01$) (**Figure 11**).

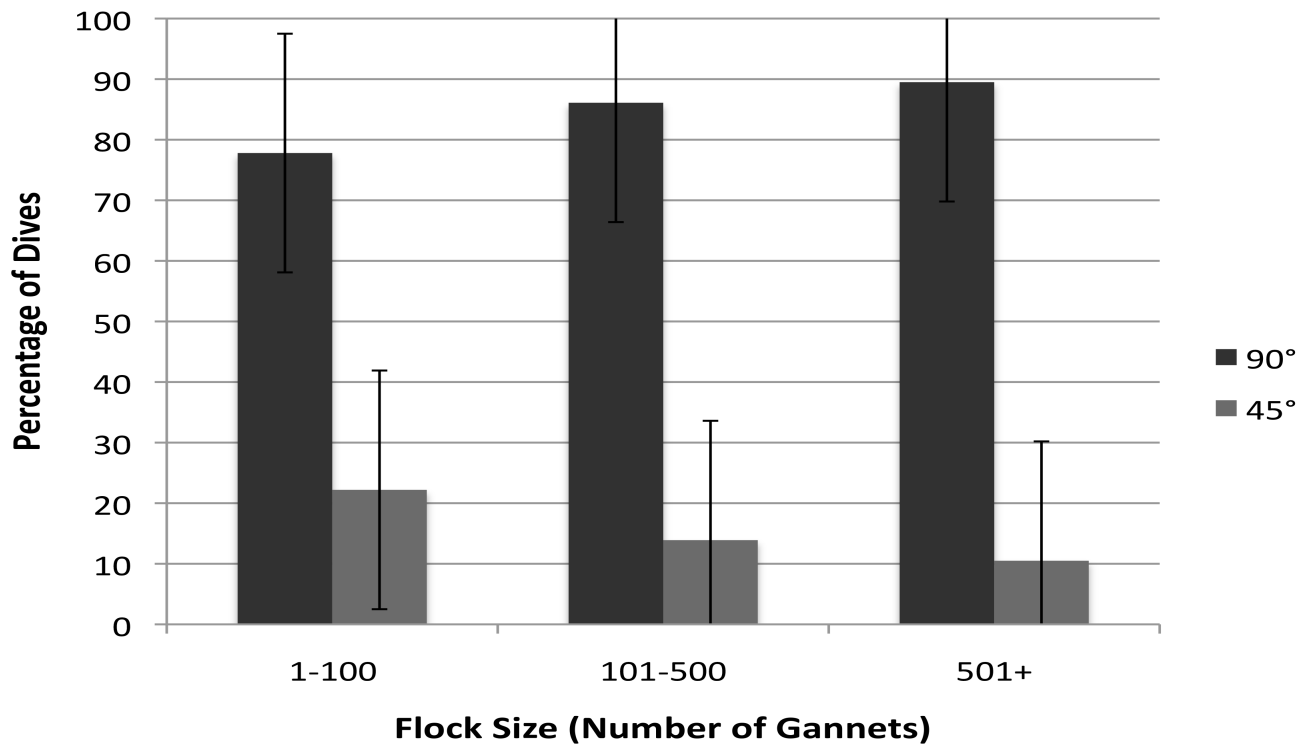


Figure 11. The percentage of dive angles recorded in different sized flocks of foraging gannets in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

The percentage of dives occurring at or above 5m increased with flock size. Percentages of dives initiated at or above 5m comprised 64.2% (n=654) of total dives (n=1019) in flocks with less than 100 gannets. This increased to 74.6% (n=1778) of dives in flocks with 101-500 gannets (n=2383) and increased further, to 80.8% (n=1372) of dives taken in the largest recorded flocks of 501+ birds (n=1698) (GEE: Wald test, $z = 5.74$, $SE = 0.213$, $P < 0.05$) (**Figure 12**).

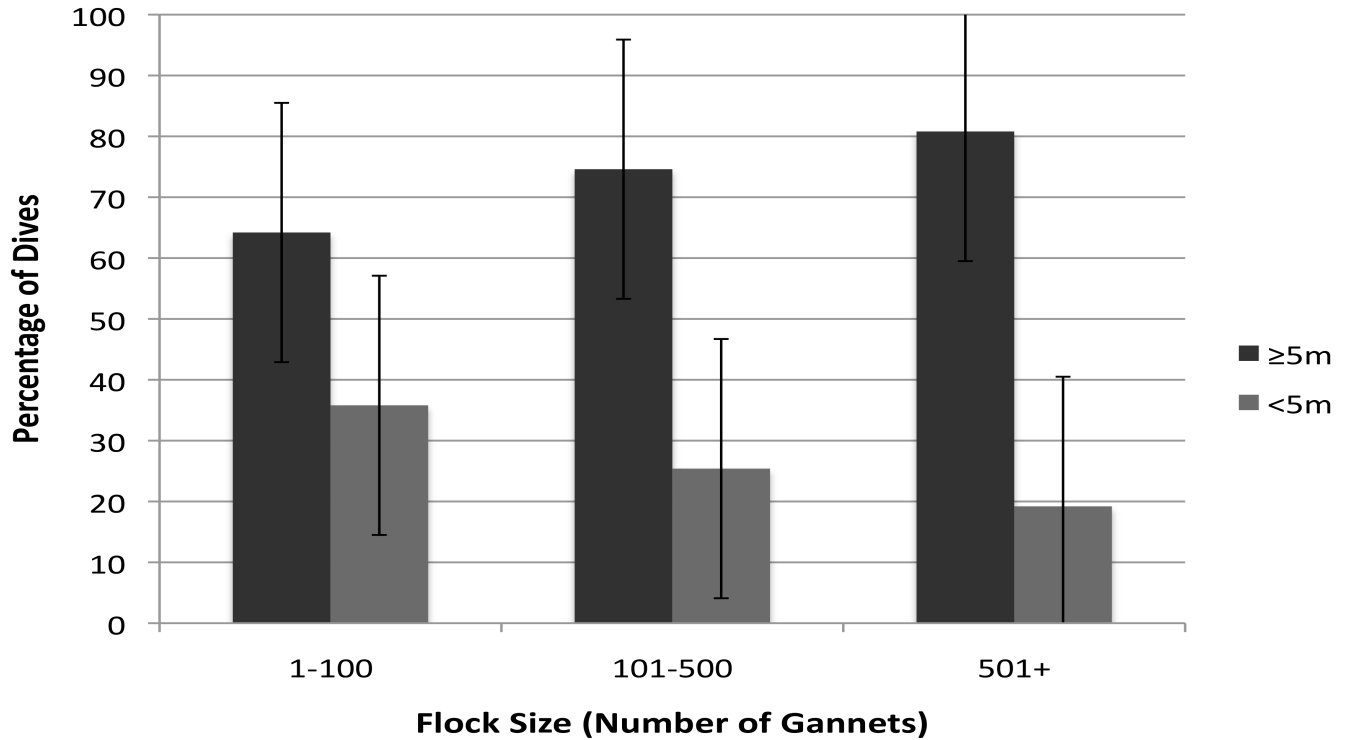


Figure 12. The percentages of dive heights recorded in different sized flocks of foraging gannets in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

The majority of dive types decrease with flock size, except 90° dives initiated greater than 5m which comprised 56.7% (n=540) of the total dives (n=952) in the smallest flocks, 70.0% (n=1469) of the total dives (n=2099) in medium sized flocks, and 75.9% (n=1074) of the total dives (n=1415) in the largest flocks (**Figure 13**).

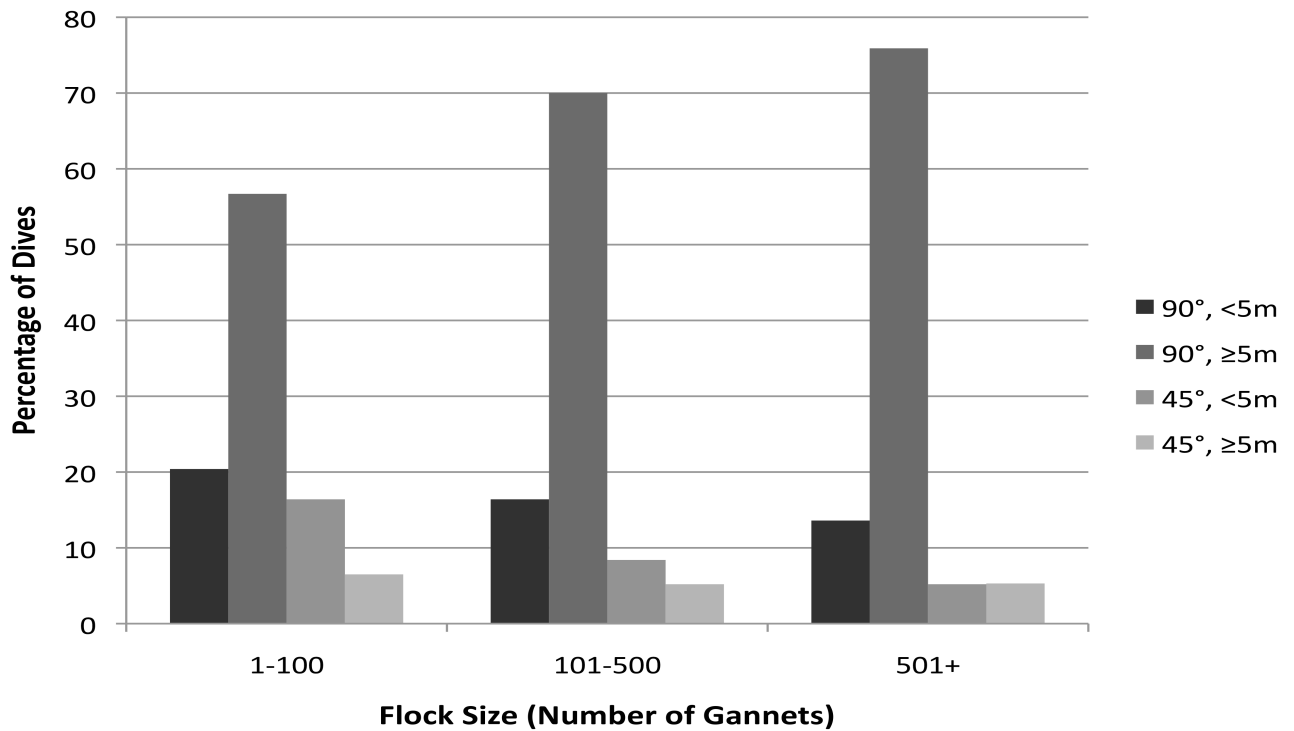


Figure 13. The total percentage of each dive tactic recorded in different foraging gannet flock sizes in the Hauraki Gulf, New Zealand.

4.4 Influence of Environmental Factors in Plunge Diving Tactics

4.4.1 Wind

Dives were completed 95.9% (n=1166) and 95.2% (n=2564) of the time in winds less than 10km/h and between 11-27km/h, respectively. However, completion decreased to 92.7% (n=1035) once winds exceeded 28km/h. While increasing wind speeds were found to have little significant effect on dive completions, there was a slight decline in the percentage of completed dives once winds were greater than 28km/h (GEE: Wald test, $z = 3.03$, $SE = 0.165$, $P < 0.1$). Of the 3563 dives recorded in winds under 27km/h, 82.0%, (n=2922) were initiated at or above 5m in altitude. Of

the 936 dives recorded in winds exceeding 28km/h, 60.5% (n=566), were initiated at or above 5 meters in altitude (GEE: Wald test, $z = 22.5$, $SE = 0.168$, $P < 0.0001$) (Figure 14).

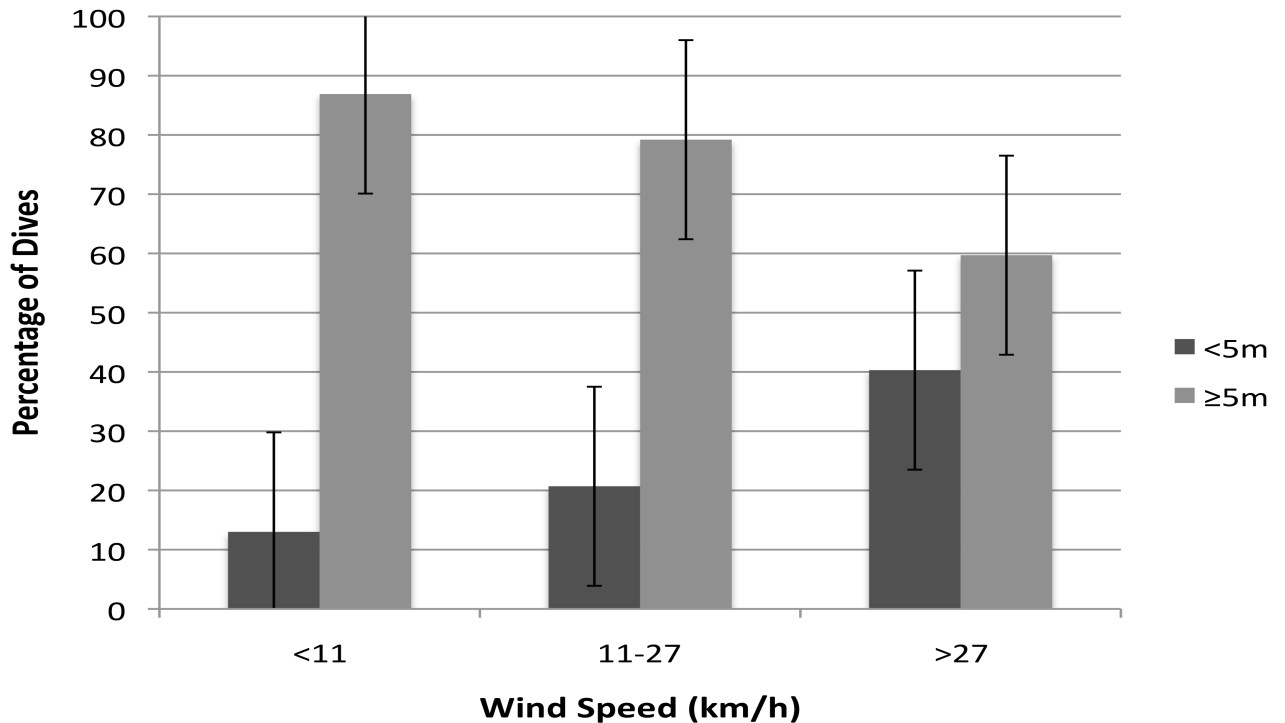


Figure 14. The percentage of dive initiation heights recorded in various wind speeds in the Hauraki Gulf, New Zealand. Bars represent Standard Error (SE).

An analysis of the wind speeds and dive angle indicated that of the 3378 dives recorded in winds under 27km/h, 88.0%, (n=2922) were 90° profiles. Of the 911 dives recorded in winds exceeding 28km/h, only 82.8% (n=754), were initiated at or above 5 meters in altitude (GEE: Wald test, $z = 5.32$, $SE = 0.124$, $P < 0.05$) (Figure 15).

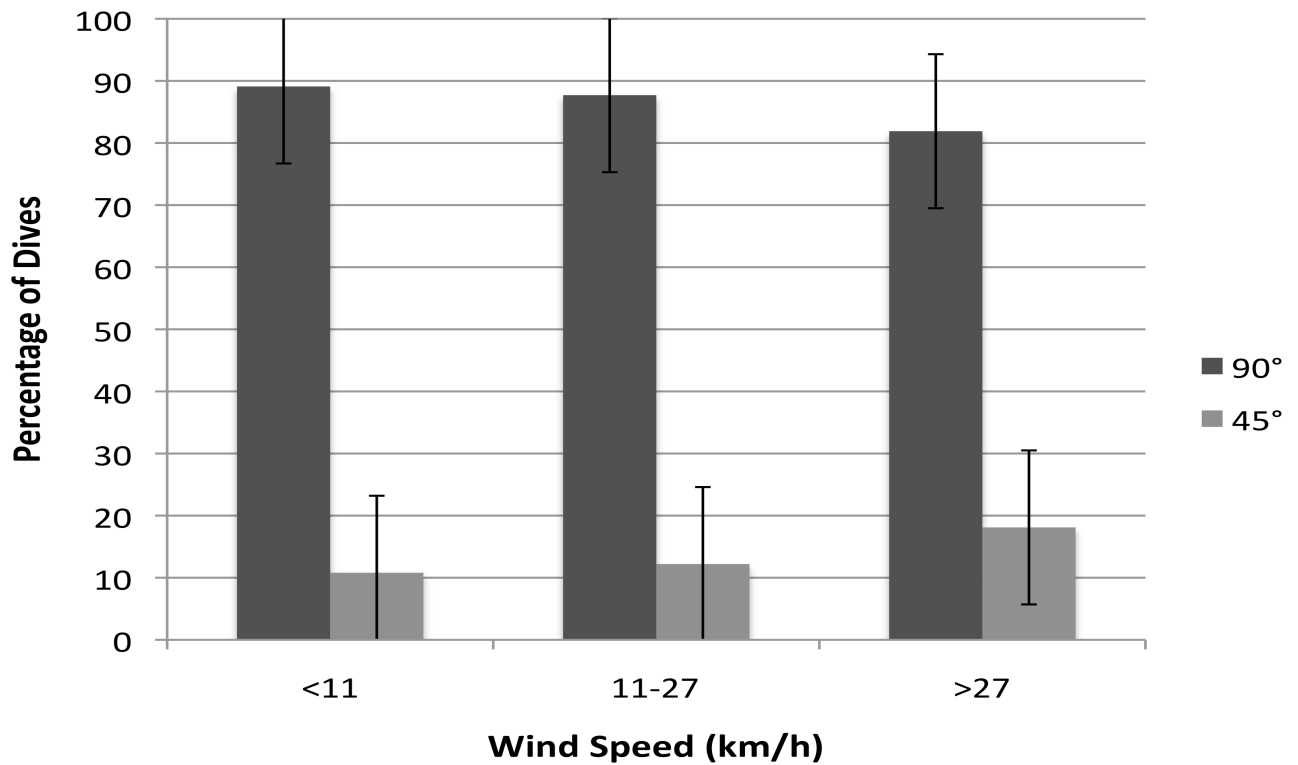


Figure 15. The percentage of gannet dive angles recorded under various wind conditions in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

Overall, the percentage of 90° dives decreased with increasing wind speeds, the percentage of 90° dives initiated <5m saw the largest degree of increased usage of all dive variations in higher wind categories (**Figure 16**).

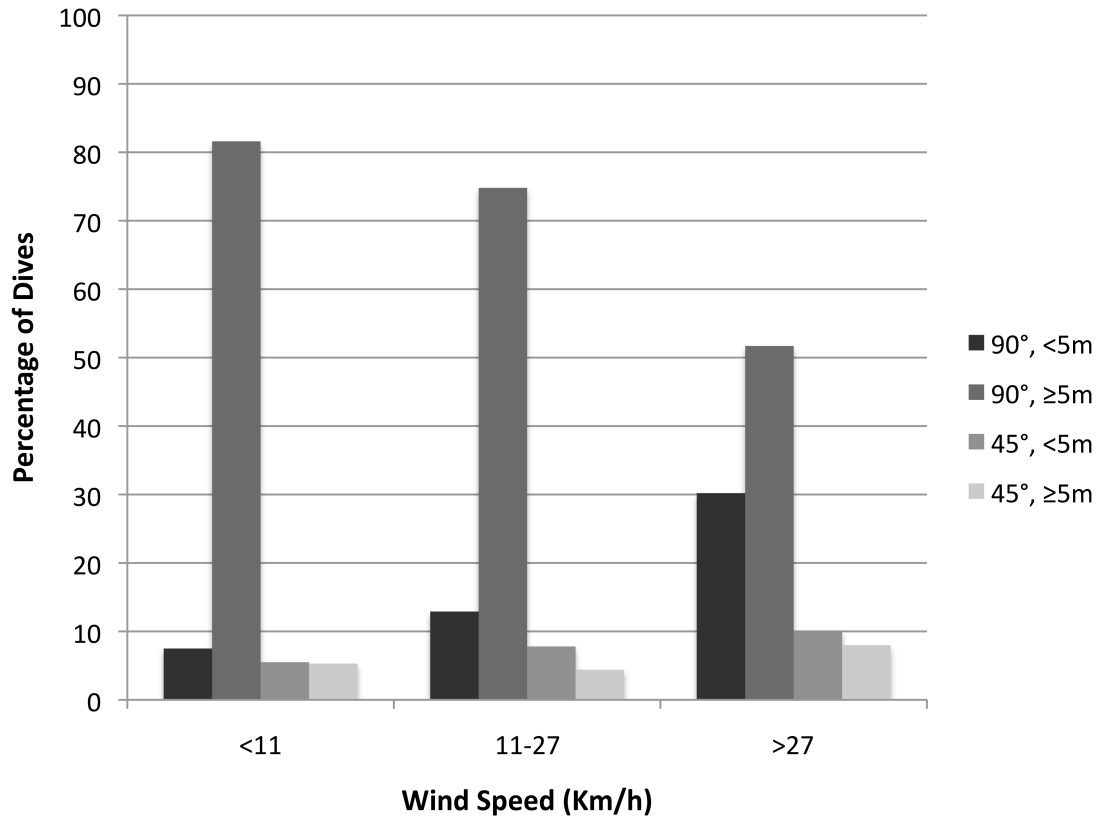


Figure 16. The total percentage of each dive tactic recorded in foraging events occurring in different wind speeds in the Hauraki Gulf, New Zealand.

4.4.2 Sea Surface Temperature (SST)

The recorded SST's ranged from 12.7 to 20.9°C (16.6 ± 2.9), with the highest number of dives occurring in 13.6°C water ($n=1062$). An analysis of SST's effect on the variations of dive tactics found no relation between dive completions and water temperatures (GEE: Wald test, $z = 2.60$, $SE = 0.04$, $P = 0.11$). However, there was a positive relation between increasing SST and the percentage of dives initiated above 5m (GEE: Wald test, $z = 3.92$, $SE = 0.08$, $P < 0.05$) (**Figure 17**).

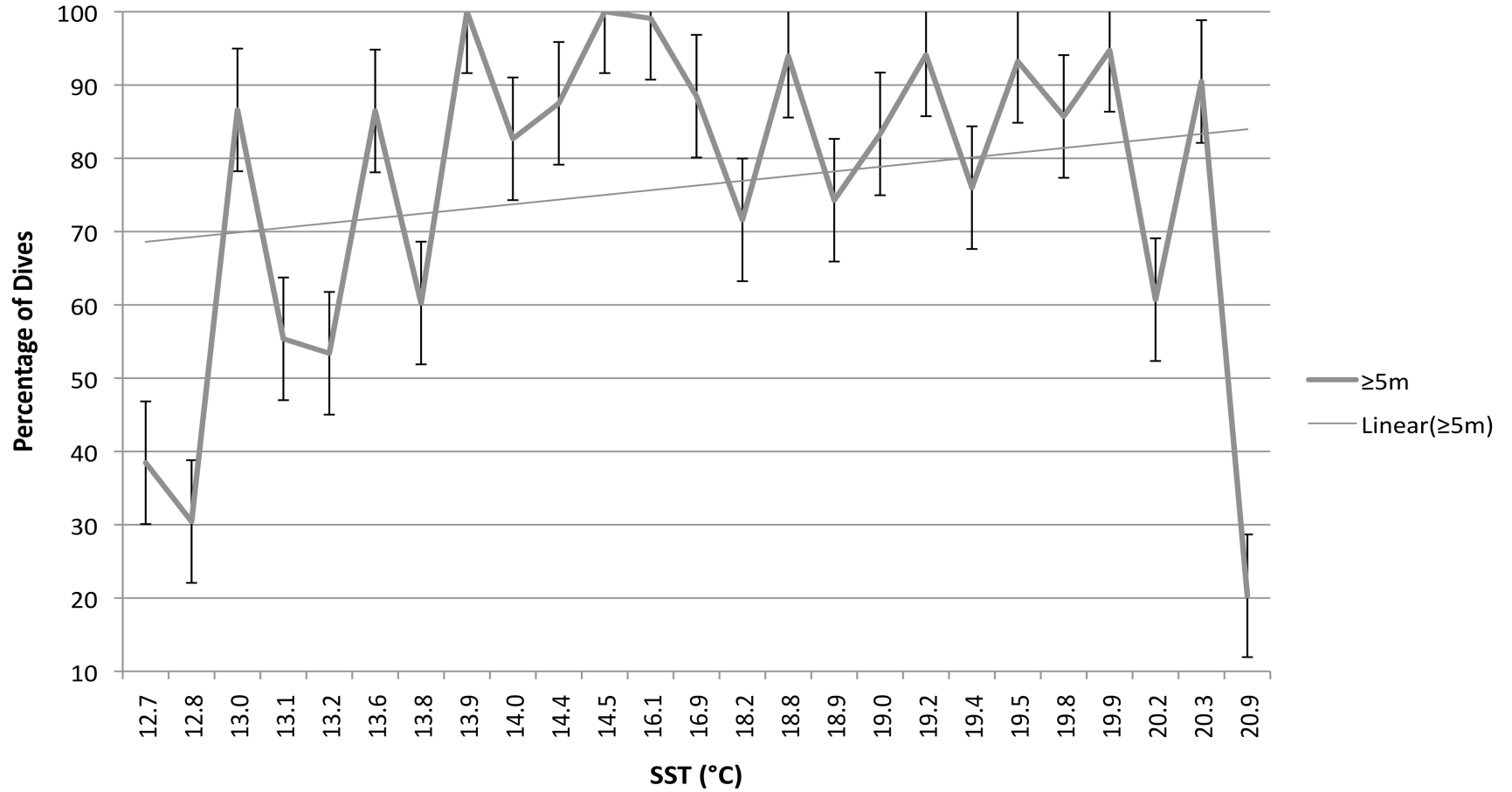


Figure 17. The variations and trend of increasing dive height frequencies in gannets in the Hauraki Gulf New Zealand, as affected by increasing SST. Bars represent standard error (SE).

SST was additionally found to be negatively related with the relative frequency of 90° dive profile angles, which decrease in frequency approximately 5.0% as temperatures increase (GEE: Wald test, $z = 9.95$, $SE = 0.07$, $P < 0.01$).

4.4.3 Water Depth

The recorded water depths ranged from 18.1 to 54.3m (37.5 ± 8.9), with the most frequently recorded number of gannet dives occurring in 34.9m water ($n=1062$). There was a positive relation between both the percentage of dives initiated above 5m and the percentage of 90° dives, with increasing depth. Trend lines indicate an approximate increase in the percentage of 90° dives by 6.0% in the range of depths between the shallowest (18.1m) and deepest (54.3m) recorded depths (GEE: Wald test, $z = 2.73$, $SE = 0.012$, $P < 0.1$). Dive height and depth was found to be highly dependent (GEE: Wald test, $z = 11.17$, $SE = 0.013$, $P < 0.001$), with the percentage of dives greater than 5m increasing in frequency almost 10.0% between the shallowest and deepest recorded depths. An analysis of water depth's effect on the variations of dive tactics found little correlation between dive completions and water depths (GEE: Wald test, $z = 1.95$, $SE = 0.015$, $P = 0.16$).

4.5 Influence of Hetero-specifics On Gannet Plunge Diving Mechanics

Of the 31 filmed feeding events, 80.6% ($n=25$) occurred in the presence of common dolphins, containing 84.0% ($n=4572$) of the total applicable recorded gannet dives ($n=5440$). Bryde's whales were present in 32.3% ($n=10$) of feeding events, and

24.9% (n=1384) of all applicable recorded gannet dives (n=5561) occurred in their presence.

4.5.1 Dolphin Pod Size Influence on Dive Mechanics

A total of 4164 completed 90° dives took place in the presence of dolphins. Of these 68% (n=2843) occurred in feeding events where more than 100 common dolphins were foraging. In contrast, of the total 734 recorded 45° dives, 80% (n=599) took place in feeding events with 100 or fewer foraging common dolphins (GEE: Wald test, $z = 8.84$, $SE = 0.107$, $P < 0.01$) (**Figure 18**).

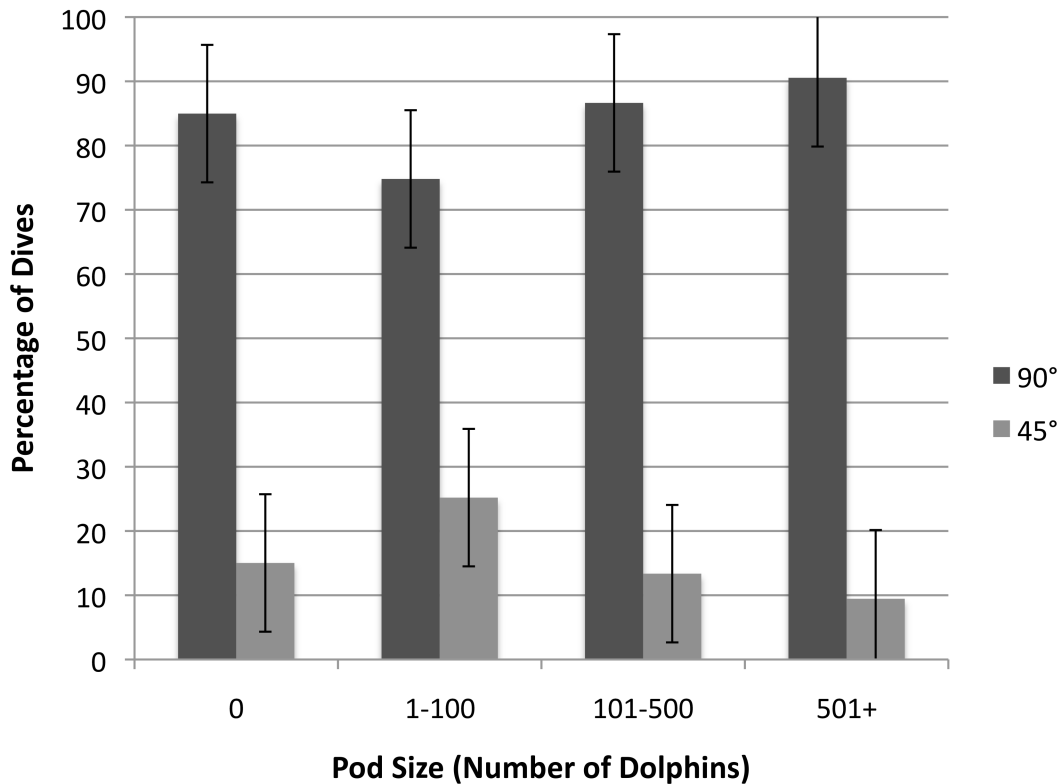


Figure 18. The percentages of gannet dive angles recorded in various dolphin pod sizes in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

Foraging pods of common dolphins with an excess of 100 individuals contained 51% (n=672) of the total low altitude gannet dives (n=1296), and 72.0% (n=2762) of the total 3804 high altitude dives (GEE: Wald test, $z = 10.88$, $SE = 0.115$, $P < 0.001$) (Figure 19).

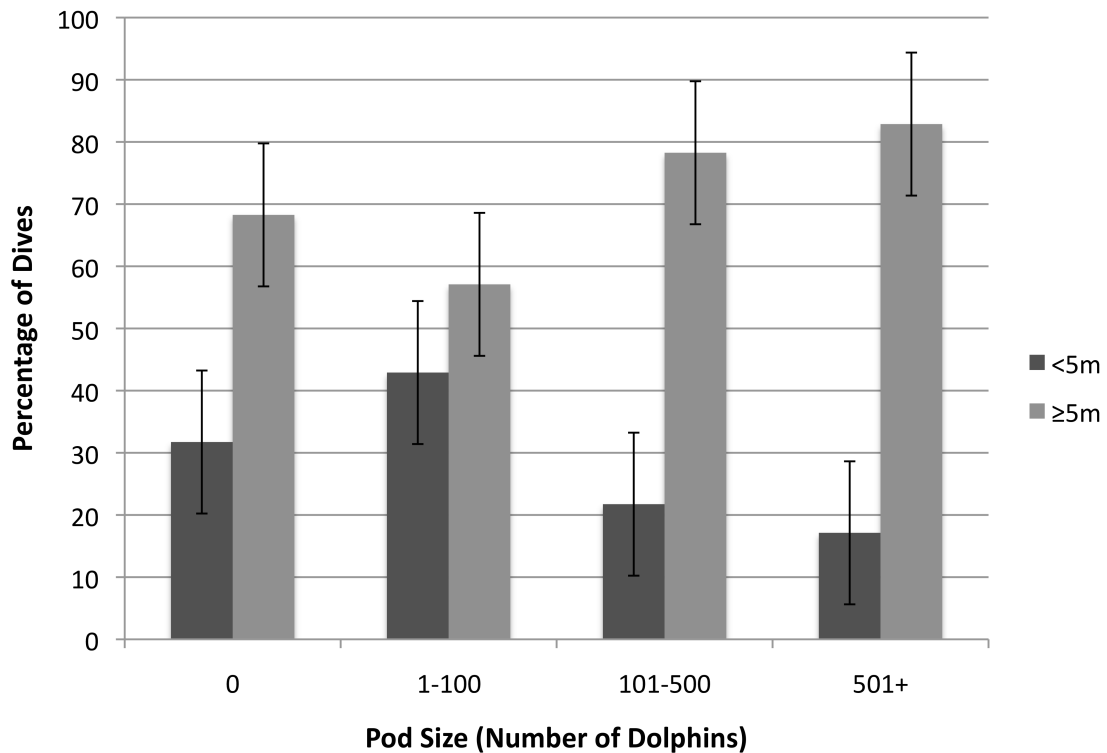


Figure 19. The percentage of gannet dive heights recorded in different sized foraging dolphin pods of in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

There was an increased preference for higher altitude 90° dives when foraging in conjunction with larger dolphin pods. When foraging in conjunction with smaller pods, higher altitude 90° dives comprised 49.2% (n=393) of the total dives (n=799). This increased to 73.8% (n=1196) of the total dives (n=1620) in medium sized pods, and 78.5% (n=1054) of the total dives (n=1342) in the largest pods (**Figure 20**).

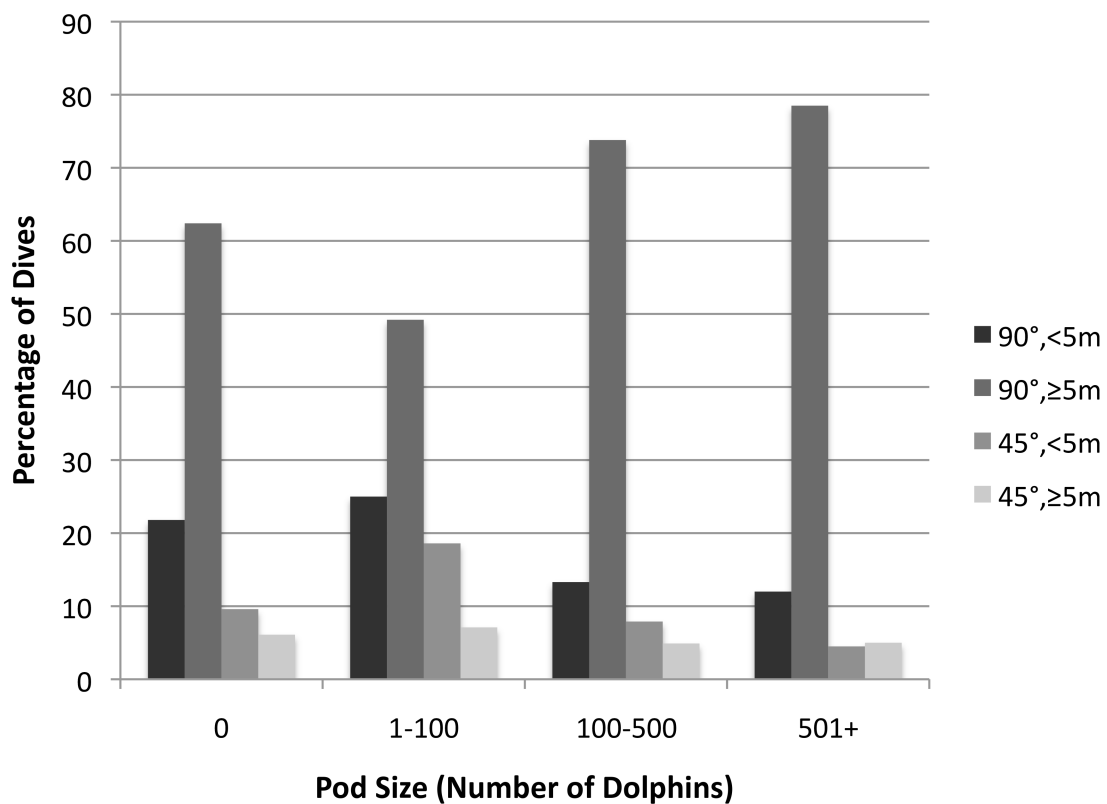


Figure 20. The total percentage of each dive tactic recorded in feeding events occurring in different sized dolphin pods in the Hauraki Gulf, New Zealand.

4.5.2 Dolphin Behaviour Influence on Dive Mechanics

There was found to be some dive mechanic variation that may be attributed to dolphin foraging behaviours, as carouselling and line-abreast foraging strategies were found to have a greater percentage of 90° dives (87.5%, and 87.6%, respectively) than dives taken during synchronous dive herding (80.3%) or when dolphin foraging strategy could not be identified (82.9%)(GEE: Wald test, $z = 0.72$, $SE = 0.22$, $P = 0.40$) (**Figure 21**).

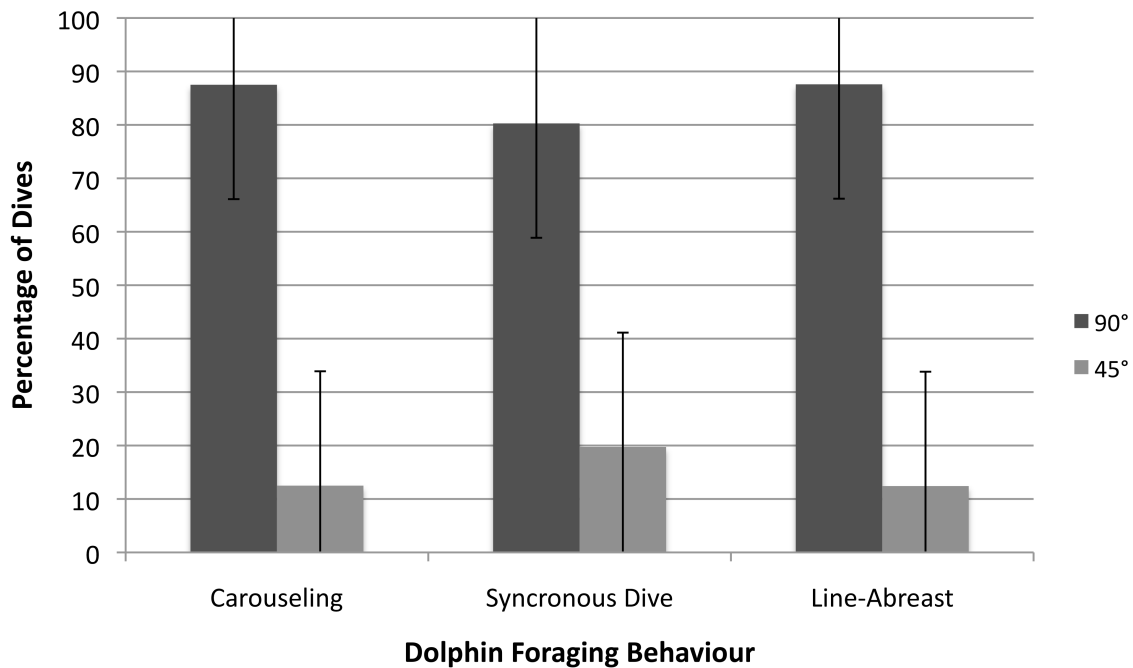


Figure 21. The percentage of gannet dive angles recorded during different dolphin foraging strategies in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

Likewise, while dive initiation heights were not determined to be heavily influenced by dolphin behaviour, the frequency of higher altitude dives during carouseling and line-abreast strategies were generally higher (79.3% and 84.1%, respectively), than dives taken during synchronous dive herding (72.0%) or when dives could not be attributed to a single dolphin foraging strategy (70.8%)(GEE: Wald test, $z = 1.28$, $SE = 0.32$, $P = 0.26$) (**Figure 22**).

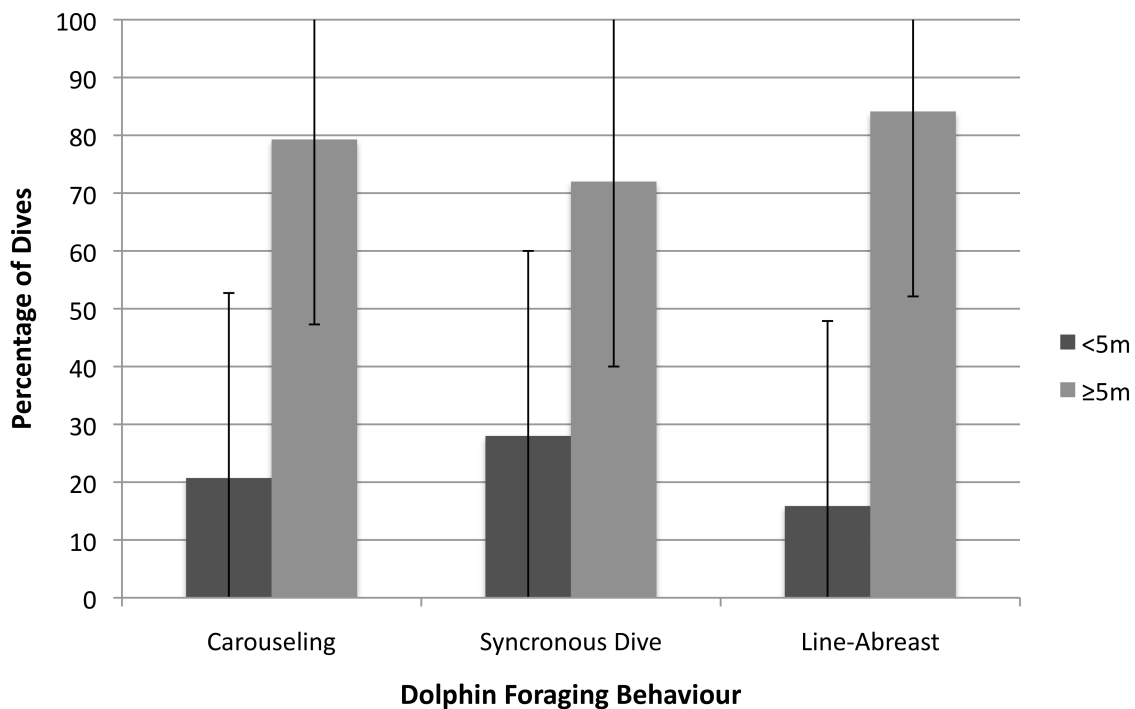


Figure 22. The percentage of gannet dive heights recorded during different dolphin foraging strategies in the Hauraki Gulf, New Zealand. Bars represent standard error (SE).

When overall gannet dive mechanics were examined in relation to dolphin foraging tactics, the majority of dive variation can be attributed to differences in low

altitude 45° dives, which comprised 7.1% (n=143) of all dives that took place during carouselling foraging tactics, increased to 17.2% (n=23) of dives during dolphins synchronous dive behaviour, and decreased to only 0.9% (n=1) of all dives recorded during line-abreast foraging tactics. The relation between gannet dive mechanics and dolphin foraging behaviour is displayed in **Figure 23**.

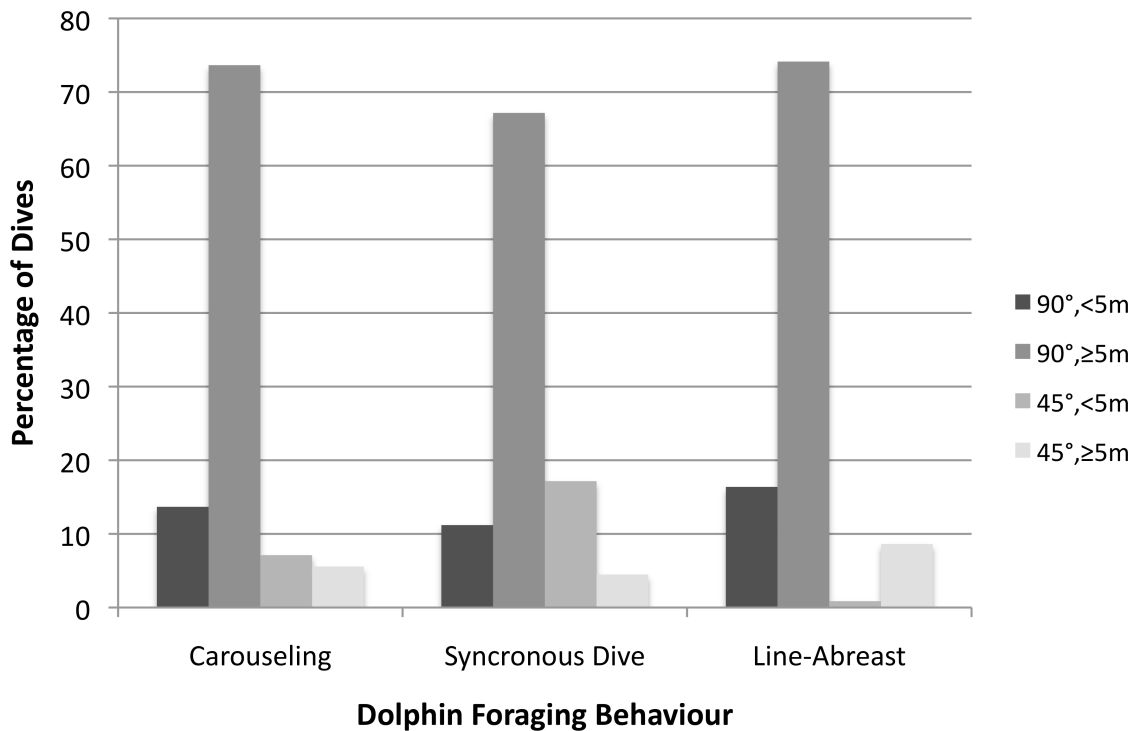


Figure 23. The relationship between dolphin foraging strategies and gannet dive mechanics.

4.5.3 Bryde's Whale Presence Influence on Dive Mechanics

Bryde's whales were only recorded as present during 21.4% (n=9) of recorded work ups (n=42). However, they were discovered to have some influence on gannet dive behaviour.

In the presence of Bryde's whales, the percentage of high altitude gannet dives decreased from 78.9%(n=3035) of the total recorded dives in their absence (n=3845), to just 61.2% (n=767) of the total dives (n=1253) when feeding in their presence (GEE: Wald test, $z = 3.22$, $SE = 0.493$, $P = 0.073$) (**Figure 24**).

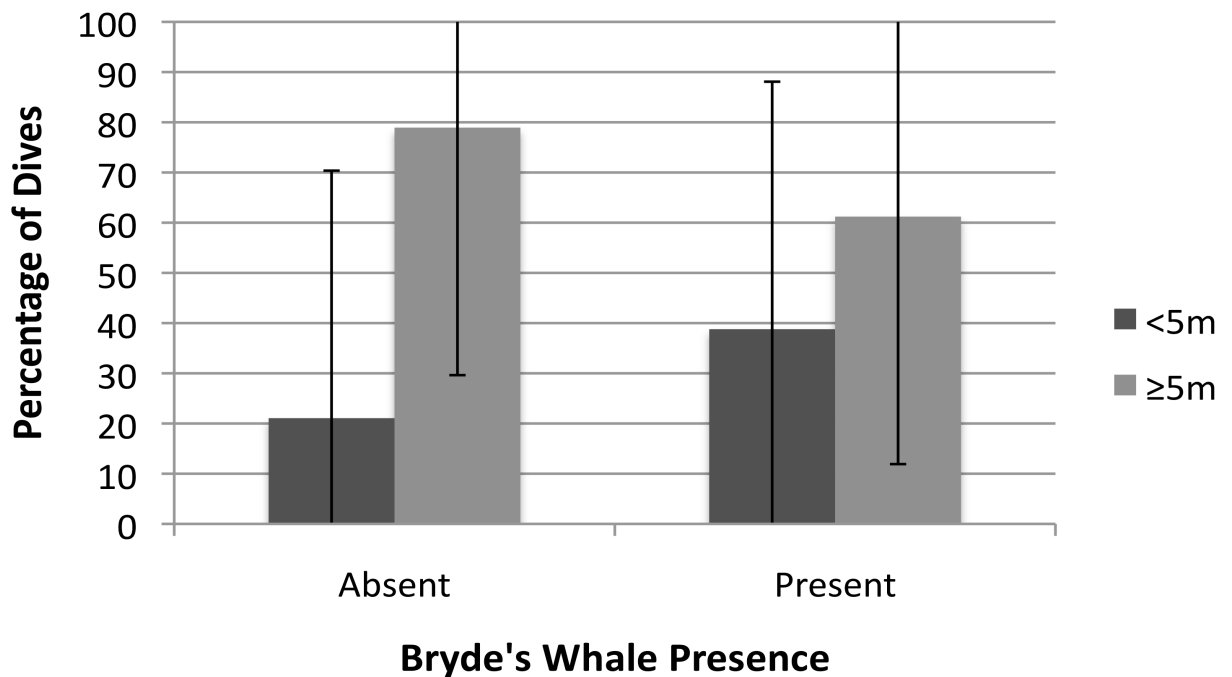


Figure 24. The relative percentage of gannet dive heights when foraging with or without Bryde's whales. Bars represent standard error (SE).

Likewise the percentage of 90° dives dropped from 87.4% (n=3207) of the total dives (n=3671) taken in the absence of the whales, to 79.3% (n=955) of the total dives (n=1205) taken in their presence (GEE: Wald test, $z = 2.74$, $SE = 0.378$, $P = 0.098$) (**Figure 25**). While a trend is evident, neither result reached statistical significance.

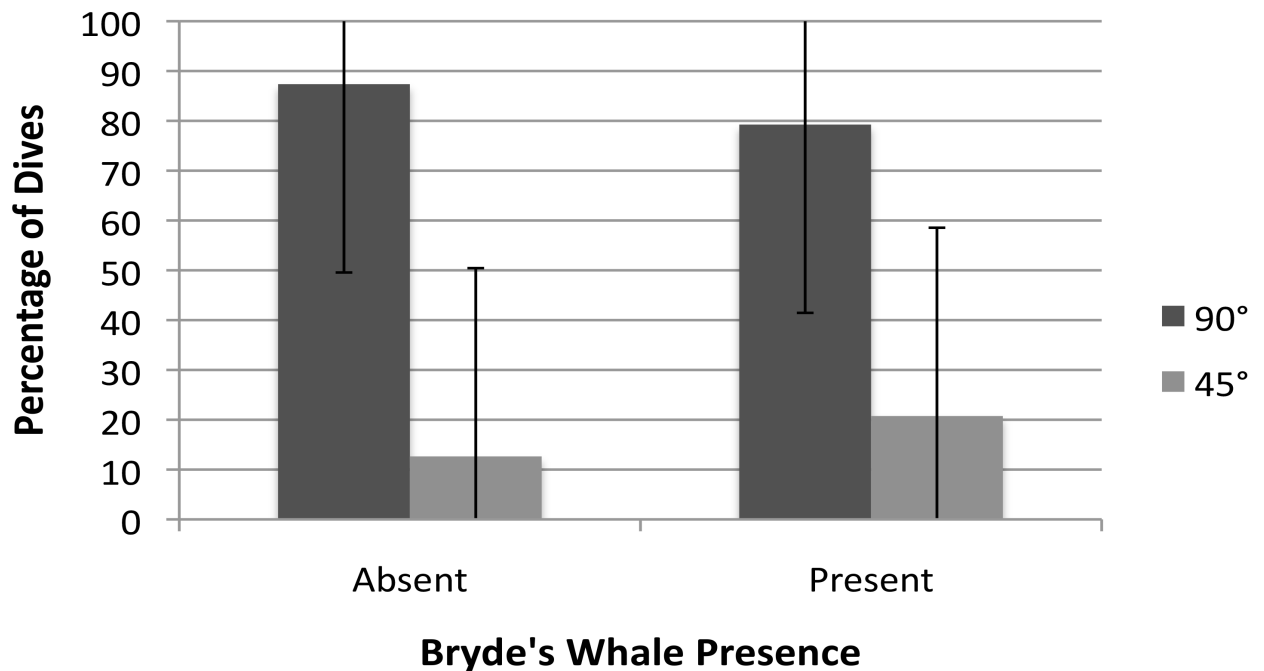


Figure 25. The relative percentage of gannet dive angles when foraging with or without Bryde’s whales. Bars represent standard error (SE).

4.5.4 Hetero-specific Seabird Presence Influence on Dive Mechanics

Whether the presence of other bird species (shearwaters, petrels, and tern species) influence dive profiles and heights was examined. Shearwater species were the most commonly associated species, and formed associations on 82.6% (n=19) of the days

filmed (n=23). Terns and shearwaters were far less likely to form associations, and were only present during 17.4% (n=4) of the filmed days.

The presence of these hetero-specific foraging bird species was shown to influence gannet foraging behaviour in some cases. Shearwater presence had the greatest effect on gannet dive variations, wherein the percentage of high altitude dives decreased from 89.9% to just 67.6% when in their presence (GEE: Wald test, $z = 17.8$, $SE = 0.378$, $P < 0.0001$) (Figure 26).

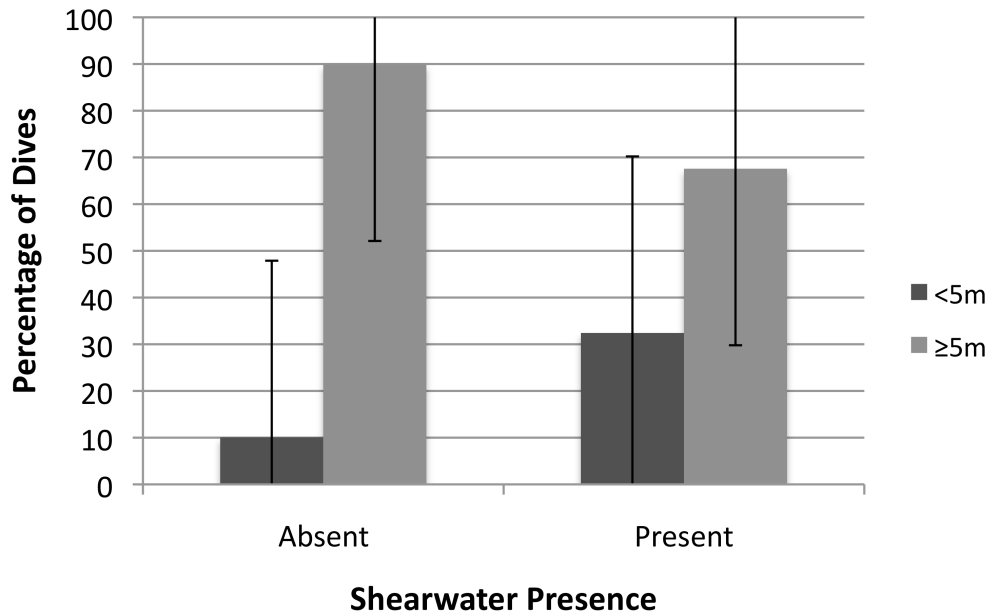


Figure 26. The relative percentage of gannet dive heights when foraging with or without shearwater species. Bars represent standard error (SE).

The presence of shearwaters was also associated with a decrease in the percentage of 90° dives from 90.2% (n=1310) in their absence to 83.4% (n=2679) in their presence (GEE: Wald test, $z = 6.43$, $SE = 0.286$, $P < 0.05$) (**Figure 27**).

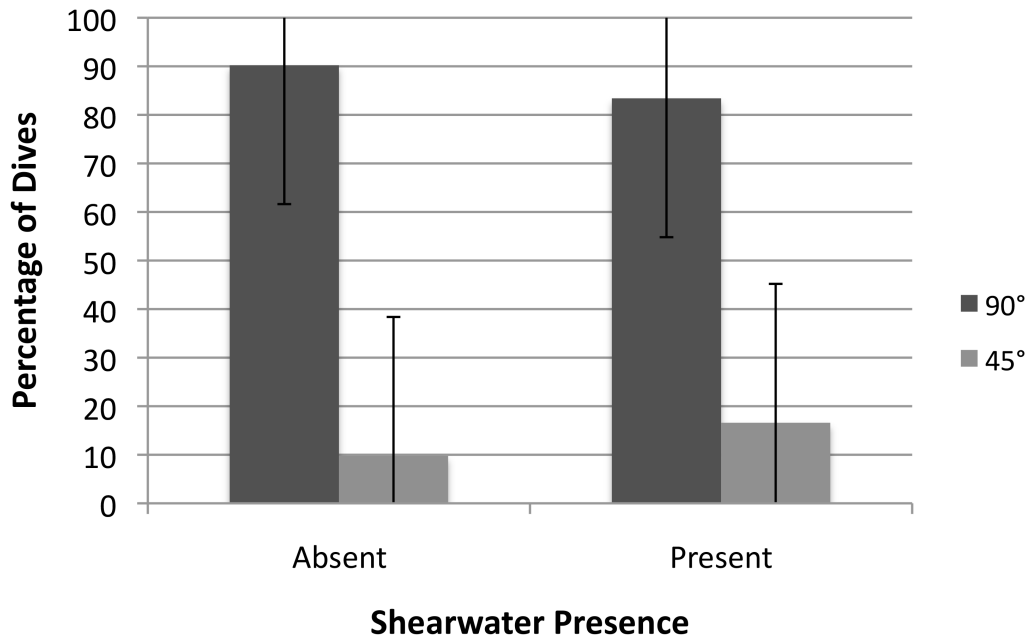


Figure 27. The relative percentage of gannet dive angles when foraging in the presence and absence of shearwater species. Bars represent standard error (SE).

In the presence of petrels, 77.7% (n=3432) of all gannet dives were initiated at or above 5m. However, in their absence, only 44.9% (n=220) of dives were initiated at or above (GEE: Wald test, $z = 6.64$, $SE = 66.9$, $P < 0.0001$) (**Figure 28**).

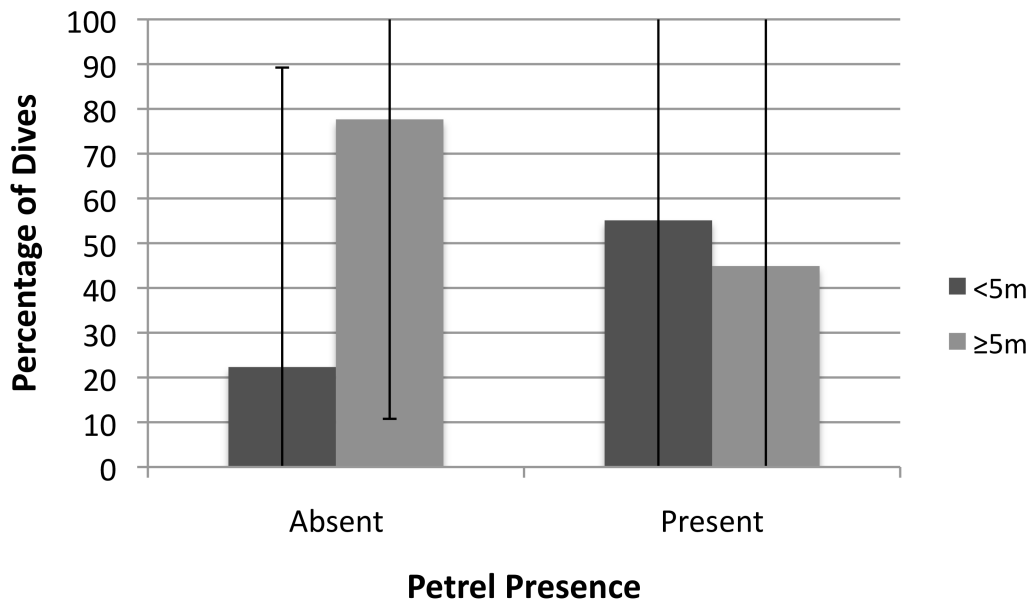


Figure 28. The relative percentage of gannet dive heights when foraging with or without petrel species. Bars represent standard error (SE).

Of all completed gannet dives recorded when foraging independent from petrel species ($n=4232$), the percentages of 90° dives was measured at 86.8% ($n=3675$). However, in the presence of petrels, the percentage of 90° dives declined to 72.7% ($n=314$) of all completed dives ($n=432$) (GEE: Wald test, $z = 5.61$, $SE = .447$, $P < 0.05$) (**Figure 29**).

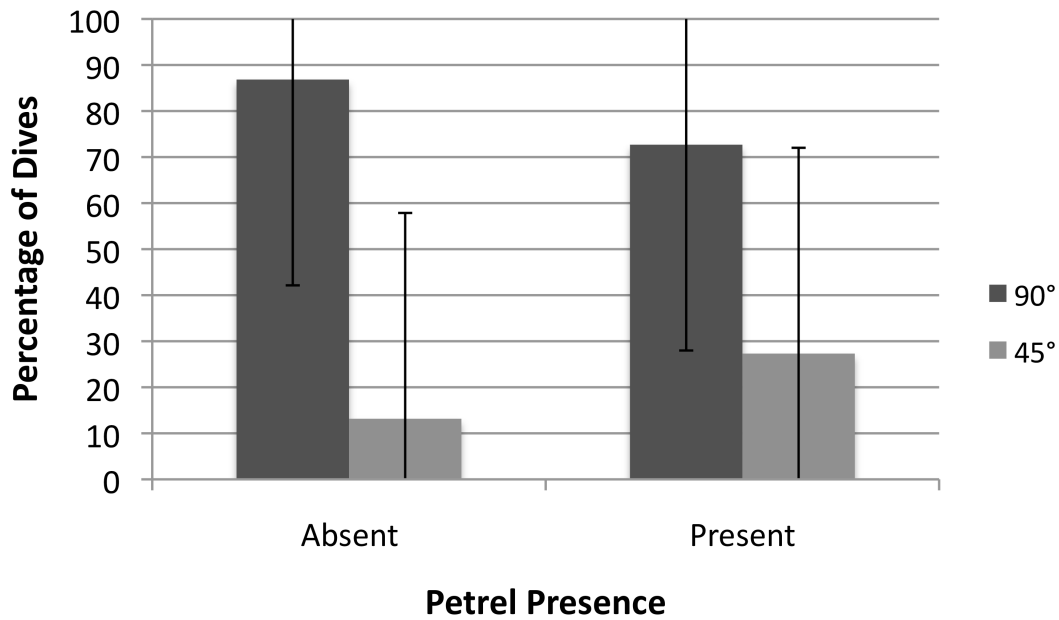


Figure 29. The relative percentage of gannet dive angles when foraging with or without petrel species. Bars represent standard error (SE).

The percentage of 90° dives increased only 2.3% when terns were present (Nested GEE: Wald test, $z = 0.11$, $SE = 0.343$, $P = 0.74$). Likewise, the percentage of dives greater than 5m was also largely unaffected by tern presence, increasing only 2.4% in their presence (GEE: Wald test, $z = 0.48$, $SE = 0.394$, $P = 0.49$).

4.6 Synchronous Diving Bout Formation

Overall initiators were shown to dive at a rate of 0.081 times per second of work up activity, or 4.86 times per minute (Wald test, $z = 265.70$, $SE = 0.15$, $P < 0.0001$). Followers overall dive frequency per time work up was reported as 0.301 times per

second, or 18.06 times per minute foraging effort within a work up (Wald test, $z = 22.61$, $SE = 0.25$, $P < 0.0001$).

4.6.1 Influence of Environmental Factors on Synchronous Diving Bout Formation

Wind speed was the only weather parameter found to be correlated with changes in the formation of synchronous diving bouts. The rate of initiation dives per time foraging was observed to decrease only slightly with increasing winds. The rate of initiation dives declined to a ratio of 0.9 (CI95%=[0.4, 2.2]) in medium winds (11-27km/h), and remained at this level (RR= 0.9, CI95%=[0.3, 2.4]) in high winds (>27km/h). However, these results were not statistically significant ($p=0.96$).

When compared to the rate of follower dives in low winds (<11km/h), the rate of follower dives decreased in moderate winds (11-27km/h) to a ratio of 0.7 (CI95%=[0.2, 2.9]). This rate was largely maintained in high winds (>27km/h) where the rate ratio was also 0.7 (CI95%=[0.2, 3.2]). However, again this did not reach statistical significance ($p=0.87$).

4.7 MSFA's Species Composition influence on Dive Synchrony Bout Formation

4.7.1 Gannet Flock Size Influence on Synchronous Diving Bout Formation

The rate of initiation dives per time foraging increases with the size of the foraging gannet flocks. When compared to the smallest foraging flocks (<100 birds), the rate increases 1.7 times (CI95%=[1.0, 2.9]) for medium flocks (100-500 birds), and doubled (RR=2.1, CI95%=[0.9, 4.7]) for large flocks (500+ birds). The results

however, are not statistically significant ($p=0.08$). (**Figure 30**).

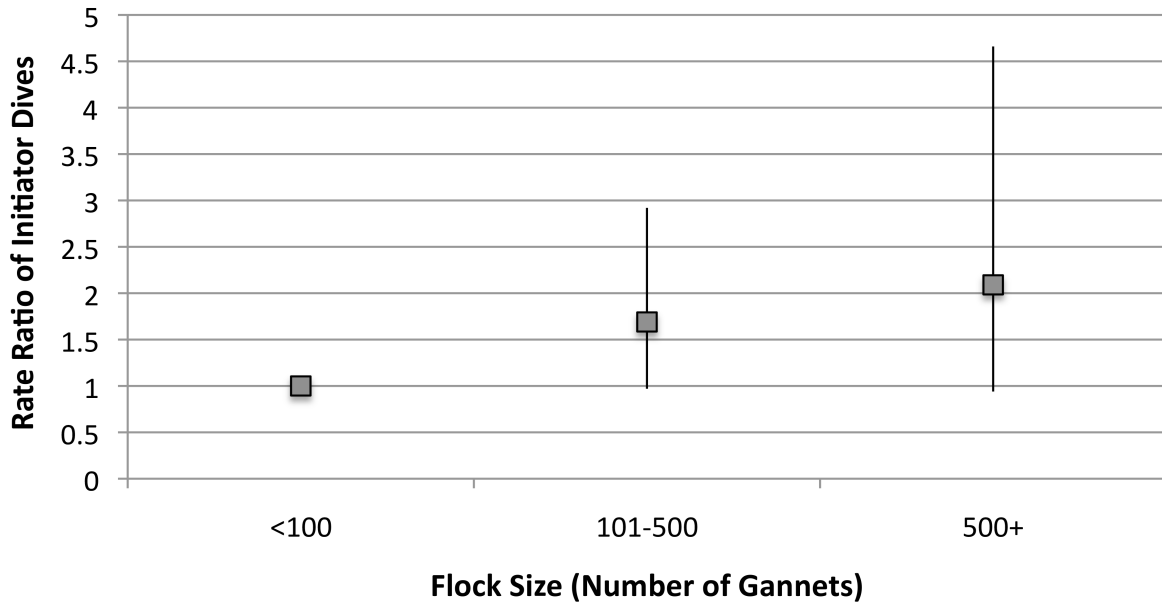


Figure 30. The relative change in the rate of initiator dives as gannet flock sizes increase. Bars indicate confidence interval of 95%.

Similarly, the rate of follower dives per time foraging also increased with the size of the foraging gannet flocks. When compared to the smallest foraging flocks (<100 birds), the rate increased 3.1 times ($CI_{95\%}=[1.3, 7.5]$) for medium flocks (100-500 birds), and quadrupled ($RR=4.3.1$, $CI_{95\%}=[1.4, 13.3]$) for large flocks (500+ birds). These results were statistically significance ($p<0.05$) (**Figure 31**).

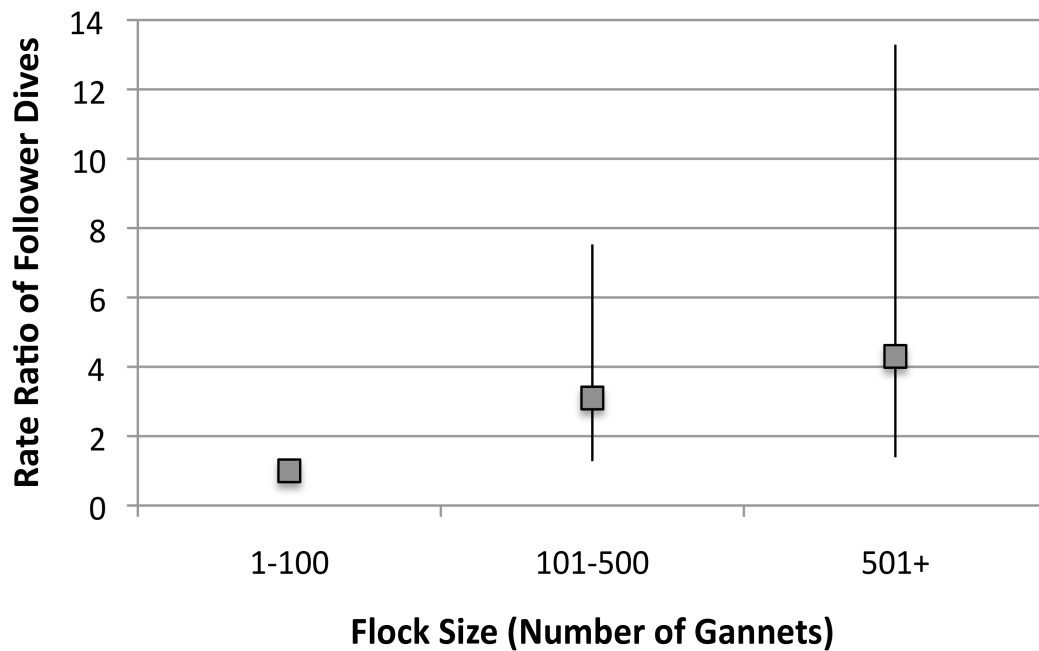


Figure 31. The relative change in the rate of follower dives as gannet flock sizes increase. Bars indicate confidence interval of 95%.

The percentages of synchronous dives were determined to increase with the number of foraging gannets in the flock. In the smallest flock (<100 birds) 55.7% (n=609) of all recorded dives (n=1094) were synchronous. The percentage of synchronous dives increased to 73.0% (n=1740) of all recorded dives (n=2384) in medium sized flocks (101-500 birds). The largest flocks had similar synchronous dive percentages, with 72.8% (n=437) of all recorded dives (n=1607) being performed in synchrony (GEE: Wald test, $z = 15.20$, $SE = 0.093$, $P < 0.0001$) (**Figure 30**).

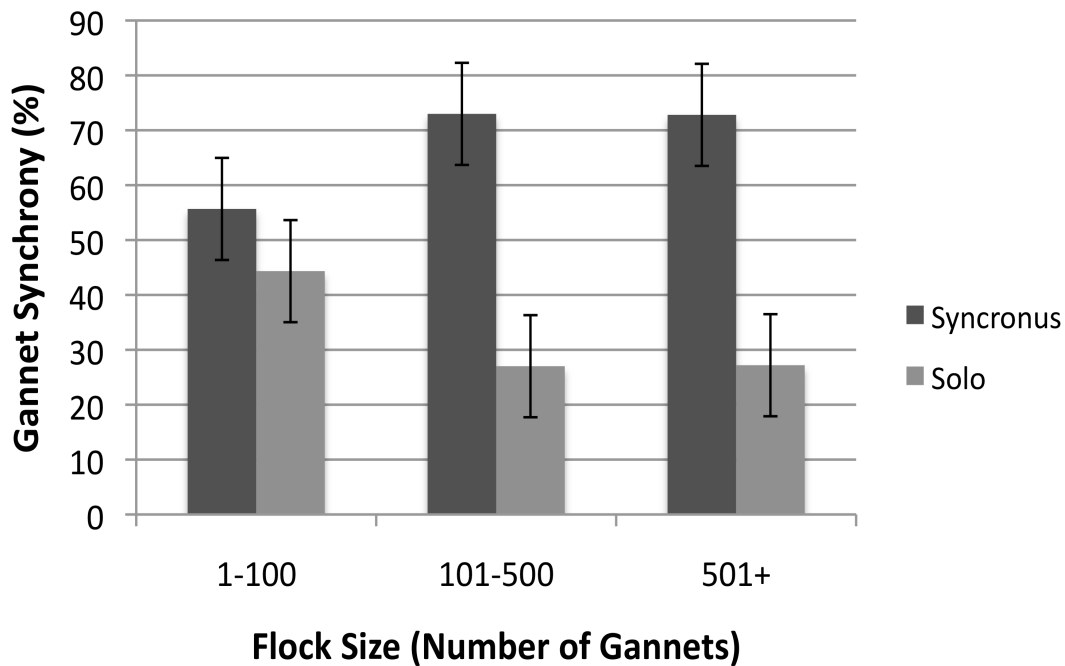


Figure 32. The percentage of synchronous dives performed in foraging flocks of gannets of varying size. Bars represent standard error (SE).

4.7.2 Dolphin Pod Size Influence on Synchronous Diving Bout Formation

The rate of initiation dives per time foraging was found to fluctuate little with the size of the foraging dolphin pods. When compared to foraging aggregations in which no dolphins were present, gannet initiation dives were less frequent by a ratio of 0.6 (RR=0.4, CI95%=[0.2, 0.8]) when foraging with small pods (<100 dolphins). The rate of gannet initiator dives was similar, however, in medium (100-500 dolphins), and large pods (>500 dolphins) with rate ratios of 0.8 (CI95%=[0.4, 1.6]) and 0.9 (CI95%=[0.4, 2.1]), respectively. These results were found to reach a level of some statistical significance ($p < 0.05$) (**Figure 33**).

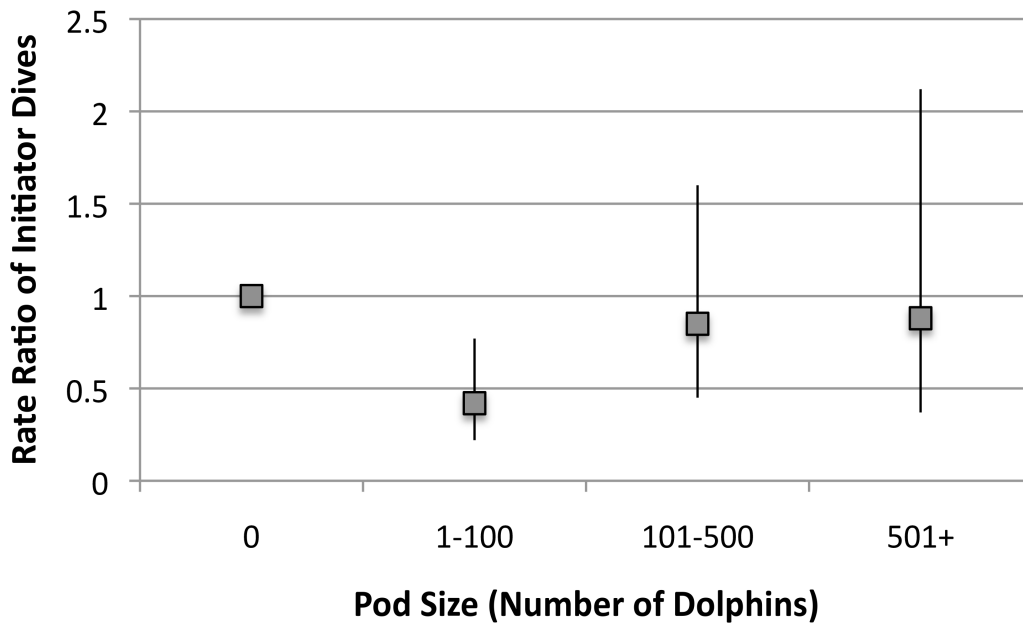


Figure 33. Gannet initiator diving rate ratios as dolphin pod sizes increases.

Bars indicate confidence interval of 95%.

The rate of gannet follower dives per time foraging was found to mirror the initiation rates of dives when foraging with dolphin pods of varying sizes. When compared to foraging aggregations in which no dolphins were present, gannet initiation dives were less frequent by a ratio of 0.8 (RR=0.2, CI95%=[0.1, 0.7]) when foraging with small pods (<100 dolphins). The rate of gannet Initiator dives was similar in medium (100-500 dolphins), and large pods (>500 dolphins) with rate ratios of 1.0 (CI95%=[0.3, 2.8]) and 1.1 (CI95%=[0.3, 3.8]) respectively. These results were found to reach a level of some statistical significance ($p < 0.01$) (**Figure 34**).

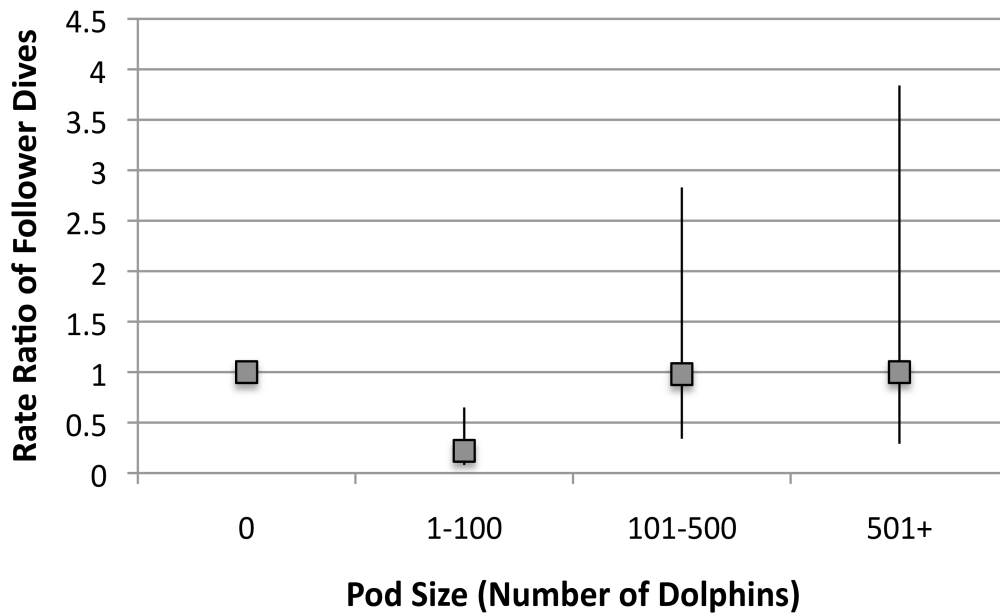


Figure 34. Gannet follower diving rate ratios as dolphin pod sizes increases.

Bars indicate confidence interval of 95%.

The percentages of synchronous dives were determined to decrease significantly only when gannets were foraging with the smallest dolphin pods. In absence of dolphins, synchronous gannet dives accounted for 74.9% (n=633) of the recorded dives (n=845). This decreased to only 50.2% (n=466) of all recorded dives (n=928) in the smallest foraging pods (<100 dolphins). The percentage of synchronous dives increased to 74.6% (n=1342) of all recorded dives (n=1800) in medium sized pods (100-500 dolphins). The largest dolphin pods had similar synchronous gannet dive percentages, with 71.3% (n=1078) of all recorded dives (n=1512) being synchronous (GEE: Wald test, $z = 0.58$, $SE = 0.120$, $P = 0.445$) (Figure 35).

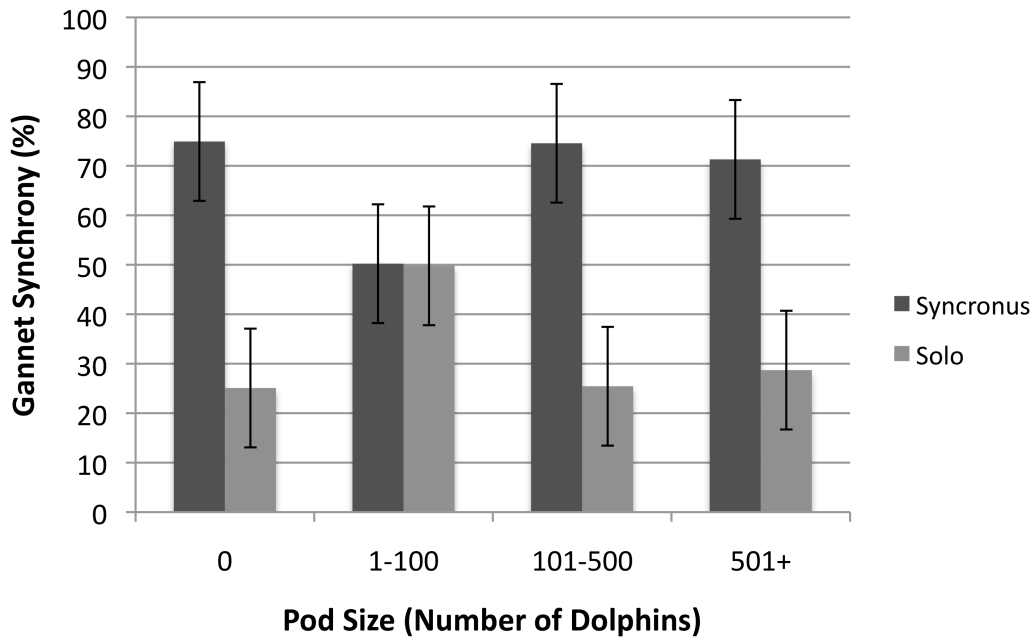


Figure 35. The percentage of synchronous dives performed in with foraging dolphin pods of varying size. Bars represent standard error (SE).

4.7.3 Dolphin Behaviour Influence on Synchronous Diving Bout Formation

Dolphin foraging tactics were associated with variations in gannet synchrony behaviours. During dolphin carouselling behaviour, 13.4% (n=295) of recorded gannet dives were initiators, 58.1% (n=1271) were followers, and the remaining 28.5% (n=623) of dives were solo dives (GEE: Wald test, $z = 0.68$, $SE = 0.12$, $P = 0.41$). Gannet synchrony was similar during dolphin synchronous dive behaviour, wherein initiator dive percentages increased to 17.4% (n=26), and follower dives decreased to 49.7% (n=74) of dives, and solo divers made up the remaining 32.9% (n=49) of the dives (GEE: Wald test, $z = 0.04$, $SE = 0.15$, $P = 0.84$). Gannet synchrony behaviour differed more radically during dolphin line-abreast foraging behaviours,

as initiator dives made up 13.6% (n=19) of the dives, and follower dives only 37.9% (n=68) of the dives. Solo dives then accounted for 48.6% (n=140) of all dives that took place during line-abreast (GEE: Wald test, $z = 2.28$, $SE = 0.28$, $P = 0.13$) (**Figure 36**).

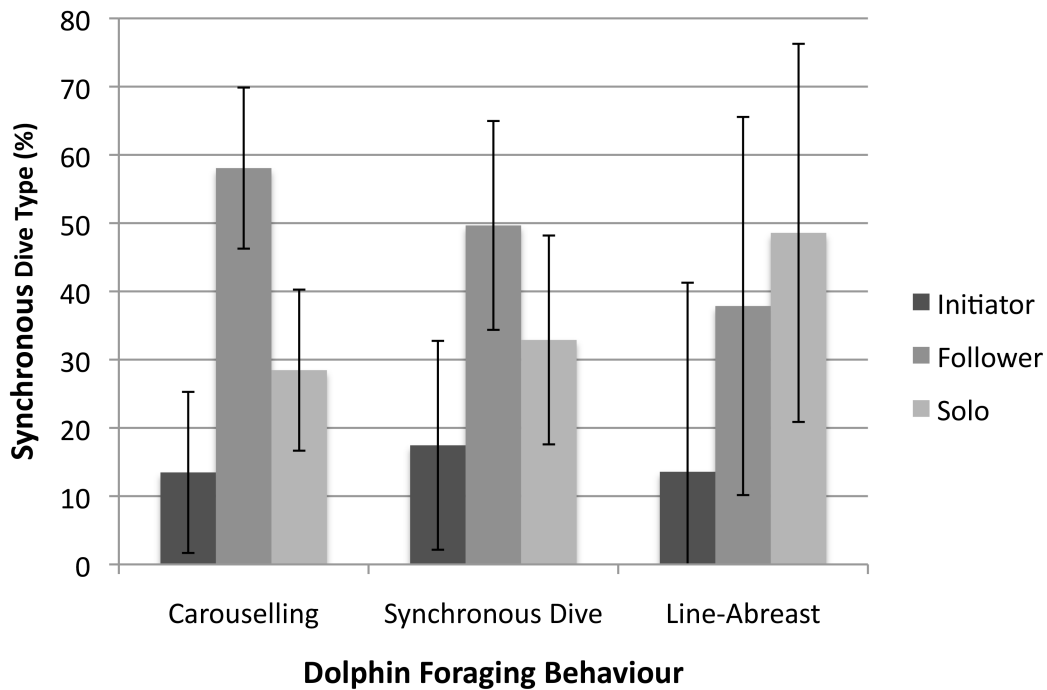


Figure 36. The relationship between synchronous gannet dive behaviour and dolphin foraging strategies. Bars represent standard error (SE).

4.7.4 Bryde's Whale Influence on Synchronous Diving Bout Formation

Bryde's whale presence had little influence on gannet dive synchrony, with synchrony rates declining from 70.1% (n=2645) of dives in their absence (n=3771) to 66.6% (n=874) of the dives taken in their presence (n=1312) (GEE: Wald test, $z = 0.34$, $SE = 0.25$, $P = 0.56$) (**Figure 37**).

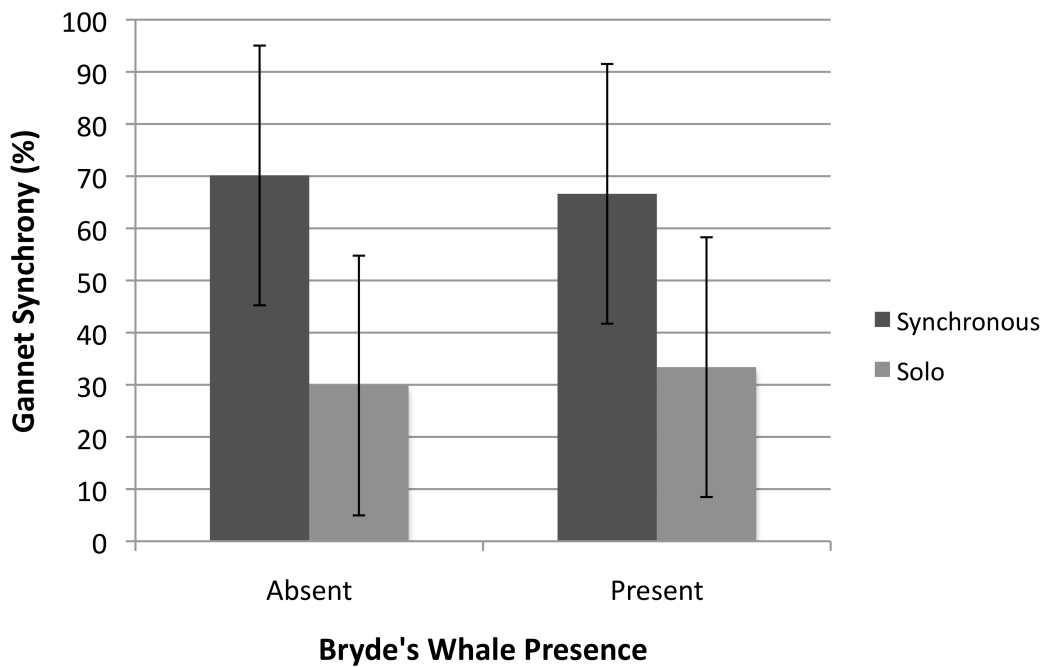


Figure 37. The influence of Bryde’s whale presence on the percentage of Synchronous dives performed in feeding events. Bars represent standard error (SE).

4.7.5 Hetero-specific Seabird Presence Influence on Synchronous Diving Bout Formation

Gannets initiator rate ratio halved to 0.5 (CI95%=[0.2, 1.0] $P<0.05$) in the presence of terns, and the rate of follower dives decreased to a ratio of 0.3 (CI95%=[0.1, 0.8] $P<0.05$) when terns were present at feeding events.

In the presence of foraging petrels, initiator gannets dives per unit foraging time increased by a ratio of 1.4 (CI95%=[0.8, 2.5] $P=0.3$), and follower dive rates increased by a ratio of 1.7 (CI95%=[0.7, 3.9] $P=0.25$).

Shearwater species had the least effect on the rate of synchronous dives, with gannet initiator dive rates increasing by a ratio of 1.1 (CI95%=[0.6, 2.2] $P=0.7$) in the

presence of shearwater species, and follower dive rates decreasing to a ratio of 0.9 (CI95%=[0.4, 3.3]P=0.9) in their presence.

5.0 Discussion

5.1 Diving Mechanics

Plunge diving is central to gannet foraging success (Garthe et al. 2000; Ropert-Coudert et al. 2004; Machovsky-Capuska et al. 2011b; Wang et al. 2013). In order to accommodate for the energy requirements faced by central-placed, homeostatic marine foragers, plunge diving behaviour must be as energetically profitable as possible, as the behaviour itself is energetically taxing (Kooyman & Ponganis, 1998; Brewer & Hertel, 2007). As such, gannets have developed two primary dive profile variations (90° and 45°), in order to maximise the energetic pay off of each dive attempt (Garthe et al. 2000; Machovsky-Capuska et al. 2011b; Machovsky-Capuska et al. 2012b). Each of the dive variations carries with it different energetic tradeoffs, where 90° dives take more time to complete than 45° dives, and expend more energy during a phase of active prey pursuit, they are more likely to result in prey capture; and are more likely to yield a higher number of captured prey per dive (Machovsky-Capuska et al. 2011b). It has been determined that per unit time spent carrying out each of the dive profiles, both dive profiles are of equal efficiency when prey capture success is taken into account (Machovsky-Capuska et al. 2011b).

The findings of this study suggest however, that gannets foraging in association with marine mammals are most likely to dive at a 90° angle to the water. It is likely that feeding in association with marine predators increases the density of fish, and makes them more accessible to gannets at the surface. As such, gannets take an increased number of 90° dives in order to capitalise on increased prey availability, collecting more numerous fish per dive, with less need for individual fish pursuit.

The relationship between the dive profile and the height at which the dive is initiated, are consistent with previous findings (Machovsky-Capuska et al. 2013b) that suggest a relationship exists between dive angles, and dive heights. In all cases within this study, the proportion of dives $\geq 5\text{m}$ was highest when the angle of entry was 90°. These findings suggest that dive profiles are indeed decided prior to dive initiations, with more vertical dives preferentially being taken from higher altitudes.

That gannets may select their dive profiles prior to initiation is further evidenced by the examination of dive abortion rates. The findings examined within this study show incredibly low dive abortion rates. This suggests that once a gannet shows intention to dive, (by tilting its wings or significantly lowering its body toward the water), it is nearly always committed to carrying the dive through to completion. This commitment to carrying through on a dive may be done in an attempt to avoid unnecessary energy expenditure. While it has been suggested that the most energetically costly portion of plunge diving is the subsequent takeoff from the water (Garthe et al. 2000; Weimerskirch et al. 2000), others have advanced the theory that the dive itself is the most energy expensive (Lovvorn & Liggins, 2002;

Green et al. 2010). In either case, the gannet's commitment to the dive once initiated, suggests it is more beneficial in most cases to carry the dive to completion than to abort the dive and perform a second attempt.

Finally, showing the intention to dive, may act as a form of local enhancement. It is possible that gannets' white colouration, and the body rotation associated with dive initiations, may aid in providing other con-specifics with a visual indication of prey availability (Forsman et al. 2002; Seppänen et al. 2007; Machovsky-Capuska et al. 2014). This would only make sense in light of low dive abortion rates, as numerous dive initiations followed by high degrees of dive abortions would send false signals to other foraging gannets, and hinder the reliability of local enhancement.

5.2 Influence of Weather on Diving Mechanics

Wind speeds have a significant effect on gannet diving behaviour, as diving gannets begin to select dives of lower altitude, regardless of angle, once wind speeds exceeded 28 km/h. Additionally, there was a slight decrease in dive completions in excessive winds. This may be a direct result of decreased manoeuvrability in high winds, making prey capture more difficult, and collisions more likely. Previous studies have shown that diving from height in dense foraging groups cannot be done without some risk of fatal collision with other gannets (Machovsky-Capuska et al. 2011a). It is possible that winds in excess of 28 km/h make accurate dives from height more difficult, thus increasing the odds of fatal collisions. In order to

ameliorate the increased dive difficulties posed by higher winds, gannets shorten their dives to below 5m.

A study of the effect wind speeds had on common terns (*Sterna hirunda*) dive profiles found that they were less likely to dive for deeper prey in higher winds (Taylor, 1983). It was hypothesised that the increased wind speeds disturbed the waters surface to a point at which deeper prey became difficult to locate, making pursuit unprofitable (Taylor, 1983). While the recorded sea states were not found to have as significant an effect on gannet dive profiles as wind speeds, it is possible that increased winds may cause significant enough disturbances in the waters surface as to make deeper prey pursuit unprofitable to gannets as well.

The relationship between lower SST and increased dive heights may be a result of an increased opportunity for prey capture associated with both increased dolphin foraging activity (Stockin et al. 2008a) and increased prey activity (Fuller, 1953) linked to the winter months in the Hauraki Gulf. Previous studies have determined that while the level of plankton remains somewhat constant within the inner gulf across seasons, there is an increase in Chaetognaths in the late winter early spring months, when SST is lower (Fuller, 1953) which has a domino effect along the food chain, increasing the numbers of pelagic prey species. Subsequently, dolphin foraging behaviour increases during this time (Burgess 2006; Stockin et al. 2008a). This increase in both prey and dolphin activity likely provides gannets with greater opportunity to capture multiple prey in bait-balls of increased density, and as such they are more likely to capitalise with longer deeper dives.

The relationship between shallower water depths and decreasing dive heights is not likely due to physical limitations of diving in shallower water, as even the shallowest recorded depths were nearly double the depth at which gannets achieve neutral buoyancy (Wilson et al. 1992; Ropert-Coudert et al. 2009). It is more likely that greater depths may allow easier access to larger dolphin pods, aiding in the consolidation of more numerous bait-balls, and allowing for increased multi-prey capture dives. It has also been shown that dolphins feed longer on descending bait-balls (Vaughn et al. 2010), as such there may be increased opportunities for gannets to dive on balls formed in deeper waters.

5.3 Influence of MSFA Composition on Diving Mechanics

Gannets forage in tight multi-species associations with other seabirds, and marine mammals (Ellesat & Fricke, 2005; Stockin et al. 2008a; Stockin et al. 2009; Wiseman, 2008). These foraging associations have direct or indirect benefits to foraging gannets, as herding dolphin behaviours often localise prey that is otherwise patchily and widely distributed across the marine environment (Evans, 1982; Forcada et al. 1994; Das et al. 2000; Clua & Grosvalet, 2001; Frantzis & Herzing, 2002; Herzing et al. 2003; Psarakos et al. 2003). However, there is a negative trade off to foraging in MSFA's, as gannets must compete with each other and increased numbers of hetero-specifics. The increased density of foragers also lends itself to complicating dive paths, and increasing the odds of collision, as multiple individuals compete over a tightly packed food source (Machovsky-Capuska et al. 2011a). How gannets navigate and utilise MSFA's is not yet fully understood. This study looks to provide a more

clear interpretation of how gannets maximise energetic gains through behavioural variations when foraging in association with marine mammals, while out competing other hetero- and con-specifics.

5.3.1 Gannet Flock Size Influence on Dive Mechanics

Increasing gannet flock sizes were found to correspond to increased percentages of high, 90° dives. With increased hetero-specific competition, the need to reduce the likelihood of collisions is elevated. The selection of 90° dives may aid in decreasing subsurface collision risks by putting competing diving gannets on parallel trajectories. This hypothesis is supported by the results discussed in section 5.6.1.

Diving from greater heights may also aid in increasing visual acuity. Gannets' specialised multifocal lenses not only aid in accommodating for two separate visual environments, above and below the surface, but also aid in increasing visual acuity at increased distances (Machovsky-Capuska et al. 2012a). As such, diving from height may then allow gannets a necessary visual advantage in larger foraging flocks, decreasing the risk of underwater collisions by increasing visual clarity above the surface.

5.3.2 Dolphin Pod Size Influence on Dive Mechanics

As the size of the foraging dolphin pods decreased the number of 45° dives increased. It has been shown previously that larger pods spend a greater amount of time foraging than smaller pods, as larger groups have a greater ability to better concentrate sparsely distributed prey (Burgess, 2006). This ability to better corral

sparsely distributed prey, as well as the ability to do so for longer durations (Vaughn et al. 2010), enables foraging gannets more opportunity to target multiple fish with more successful, deeper 90° dives. Furthermore, previous studies using GPS trackers have shown that gannets will take multiple dives (4.0-4.7 per hour foraging time) during a single foraging trip (Machovsky-Capuska et al. 2013a). It is therefore likely these longer duration feeding events, associated with larger dolphin pods, afford gannets the opportunity to dive multiple times in a single event, thereby further increasing the odds of successful prey capture using high 90° dives.

Gentoo penguins, are suggested to take 45° dives from the waters surface in order to assess prey density, and will reserve 90° dives for prey pursuit (Wilson et al. 1996). It has been suggested that gannets, like gentoo penguins, may also use 45° dives to assess prey density (Machovsky-Capuska, 2012b). The increase in 45° dives during associated feedings with smaller dolphin pods may be related to the need to scout out dense prey patches in less stationary, or scattered bait-balls with fewer foraging dolphins.

5.3.3 Influence of Dolphin Behaviour on Dive Mechanics

Another factor that seems likely to affect gannet behaviour at the surface is the foraging manoeuvres of dolphins below. Each dolphin pods' coordinated herding behaviour affects the position and density of bait-balls as well as the positions of the individual dolphins.

Previous studies have indicated that foraging dolphins most frequently rely on synchronous dive and carouselling behaviour when herding fish (Burgess, 2006).

During both of these behaviours, foraging gannets are seen to prefer high 90° dives, however, the number of shallow 45° dives increases substantially during dolphins' synchronised dives. This is likely to be result of fish swimming to the surface and scattering as dolphins dive, allowing gannets to target and capture individual prey using the momentum phase of shallower 45° dives (Machovskey Capuska et al. 2011a). In comparison, carouselling keeps fish stationary and densely packed in bait-balls at the surface. Not only have gannets been found to be more likely to dive into these aggregations (Vaughn et al. 2007, 2010), but the dense stationary schools of fish afford gannets the opportunity to take more successful deep, 90° dives in pursuit of more numerous, spatially constricted prey (Machovskey Capuska et al. 2011b).

Line-abreast foraging behaviour was rarely associated 45° dives. This is likely a result of the difficulties in capturing individual fish that are being quickly pushed ahead of dolphin pods during the momentum phase of a shallower dive. Additionally the visual advantage gained from diving at greater heights (Machovsky-Capuska et al. 2012a) may be required to more accurately target non-stationary prey. As such deeper dives, from greater heights are utilised in an attempt to better target and pursue fish using the wing flapping pursuit phase rather than relying on the accuracy required of the momentum phase associated with shallower dives.

5.3.4 Influence of Bryde's Whale Presence on Dive Mechanics

While not statistically significant, Bryde's whales presence at MSFA's was associated with a decrease in high 90° dives. This is likely a direct result of feeding whales

dispersing bait-balls when lunge feeding (Wiseman, 2008). Again, decreased density of prey is associated with shallower lower dives, as gannets select scattering individuals rather than attempt multiple prey capture.

5.3.5 Hetero-specific Seabird Presence Influence on Dive Mechanics

In contrast to the benefits of foraging with Delphinids, foraging in the presence of some hetero-specific bird species appears to hinder gannet's ability to capitalise on tightly packed bait-balls. The presence of both shearwater and petrel species was associated with dramatic increases in lower dives, and more frequent 45° dives. As both of these species feed by skimming food from the waters surface and may form rafting congregations during feeding events (Morgan, 1982; Croxall & North, 1988), they may act as obstacles for diving gannets. When foraging with significant numbers of hetero-specific birds, gannets may avoid taking higher dives in order to reduce the risk of colliding with a foraging or rafting individual. Large rafting congregations may also limit gannets' access to tight bait-balls concealed bellow. As such, gannets may target individual fish with low 45° dives (Machovsky-Capuska et al. 2011b) between birds, or at the rafts' periphery. The increase in 45° dives may also be a result of increasing numbers of probing dives (Wilson et al. 1996, Machovsky-Capuska, 2012b) to compensate for a lack of visibility. This vision obscuring effect of rafting hetero-specifics has been noted in MSFA's where rafting Gulls obscured the view of Kittiwakes (Camphuysen & Webb, 1999).

5.4 Diving Synchrony

The ability to successfully communicate intention to con-specifics foraging in MSFA's is highly important to gannets. Not only are they at increased risk of fatal collisions when feeding in MSFA's (Machovsky-Capuska et al. 2011a), they are under increased competitive pressure (Camphuysen & Webb, 1999; Couzin & Krause, 2003). The ability to successfully coordinate dives in synchronous diving bouts under a variety of constantly changing MSFA's parameters is then thought to be essential to gannet foraging (Machovsky-Capuska, 2012b). The importance of synchronous dives is reflected in the rates of synchronous dives recorded per time work up activity; where synchronous dives were initiated nearly five times per minute work up time, and follower rates were nearly five times as frequent.

5.5 Influence of Environmental Factors on Synchronous Diving Bout Formation

While previous studies have shown that short-term weather variations can have heavy influences on avian foraging behaviours (Grubb, 1977; Taylor, 1983), wind speed was the only tested weather parameter found to have any effect on the formation of synchronous diving bouts. While the correlation between wind speeds and the rate of gannet initiator and follower dives was not found to be statistically significant, a trend was evident. Whereas the rate of initiator dives fell only slightly, follower dives per unit work up time decreased considerably as winds increased. This indicates that as winds increased, the formation of synchronous diving bouts remained comparatively regular, but lasted for shorter durations. As examined in section 5.2, gannets decrease the height and angle of their dives in increased winds,

either as a consequence of decreased dive control in higher winds, or as a result of decreased deep-prey visibility due to increased surface refraction disturbances. It is likely that these factors also play a role in decreasing the duration of synchronous diving bouts, as the opportunity to join in extended bouts decreases due to increased numbers of short, shallow dives of accidental collision as high winds are thought to decrease manoeuvrability.

5.6 MSFA's Species Composition Influence on Synchronous Diving Bout Formation

5.6.1 Gannet Flock Size Influence on Synchronous Diving Bout Formation

The rates of initiator and follower dives both increased with the size of the foraging gannet flock. The rate of initiation dives more than doubled between the smallest and largest flock sizes, while the rate of follower dives quadrupled. This indicates that increased numbers of foraging gannets are associated with the formation of larger, more numerous synchronous diving bouts. Meanwhile, the overall percentage of synchronous dives was shown to increase significantly in foraging gannet flocks of increasing size. While the smallest foraging flocks had comparable numbers of synchronous and solo dives, flocks with more than 100 birds were shown to have significantly greater numbers of synchronous divers

It has been shown that the size of foraging groups, feeding on patchily distributed prey, increases with the quality of the prey patch (Brockmann & Barnard, 1979; Clark & Mangel, 1984; Valone, 1989). Individual foragers are more likely to seek out and join a foraging group with more numerous con-specific foragers at a patch in a process of local enhancement (Krebs et al. 1972; Brockmann

& Barnard, 1979; Clark & Mangel, 1984). Conversely, foraging aggregations begin to disperse as individuals abandon foraging patches that decrease in quality due to decreasing prey abundance (Iwasa, 1981), or a decreasing rate of prey capture (Green, 1980). Gannets specifically have been shown to rely on local enhancement to determine the locations of active foraging aggregations by assessing the number and direction of arriving and departing conspecifics at rafting aggregations (Machovsky-Capuska et al. 2014). Larger gannet flocks are then likely formed in conjunction with larger prey sources, which are associated with increased chances of prey location (Brown, 1996), and thereby increase the number and frequency of initiator dives per unit foraging time in larger work ups.

The increase in follower dives is likely an effect of increased initiation dives in response to greater prey densities. The mechanisms local enhancement and information transfer about patch quality between conspecifics are also at work within the patch. Prey distribution within a work up is dynamic, and bait-balls form, dissipate, and move depending on a number of factors including dolphin behaviour, and foraging pod sizes (Burgess, 2006; Vaughn et al. 2010). Individuals foraging within a group use information that improves foraging, wherein the number of animals foraging and relaying patch quality information in a group increases, the time required to search out and capture prey decreases (Pitcher & Magurran, 1983; Sernland et al. 2003). This occurs because foragers within a group observe conspecifics finding food, and then capitalise on the found food location rather than continue expending energy on individually locating prey (Pitcher & Magurran, 1983; Coolen et al. 2001; Sernland et al. 2003). The transmission of foraging information

has been observed in birds wherein changes in body posture relayed foraging information to con-specifics (Coolen et al. 2001), and the accuracy of foraging information is thought to increase with the size of the foraging flock (Brown, 1988). It is therefore reasonable to assume that when one gannet gains information on where prey is most densely aggregated within a work up, and thus prey capture most likely, it's initiation dive is likely interpreted as a signal of prey availability by nearby con-specifics. These con-specifics capitalise on this initial divers find by initiating behind the lead bird and becoming followers. This chain of dives continues until there are no more birds in the vicinity to take follower dives, or the prey patch has been dispersed. These chains of followers are more likely to happen in groups with more numerous birds, and more plentiful prey, resulting in large increases in follower dive frequencies per unit foraging time as flock sizes increase.

5.6.2 Dolphin Pod Size Influence on Synchronous Diving Bout Formation

The rate of both initiator and follower dives remained largely unaffected by variations in foraging dolphin pod sizes. There was however a decrease in the rates of both follower and initiator dive frequencies associated with gannets foraging with pods containing less than one hundred dolphins. This may be the result of smaller pods decreased ability to form bait balls as frequently, long lasting, or stationary as those formed by the larger pods that congregate specifically for the purpose of foraging (Burgess, 2006; Vaughn et al. 2010). Additionally the percentages of synchronous and solo dives were found to be equivalent in the smallest pods, while gannets strongly favoured the formation of synchronous dives in all other

circumstances. This indicates the foraging efficiency of gannets may decrease when associated with smaller pods of foraging dolphins, as dives are more likely to be taken by individuals into less densely packed bait balls, and subsequently less likely to be beneficial to followers.

5.6.3 Dolphin Behaviour Influence on Synchronous Diving Bout Formation

While the percentage of initiator dives remained largely consistent across the recorded dolphin behaviours, the highest percentage of followers were recorded during dolphin carouselling behaviour. During this behaviour, dolphins corral fish into dense bait-balls while circling the periphery of the bait-ball at the waters surface (Neumann & Orams, 2003). This behaviour not only allows foraging gannets access to densely packed prey within easy diving range, but decreases the chances of underwater collision with the foraging dolphins that maintain predictable and visible circular corralling patterns at the surface.

Follower dives remained the primary dive type during dolphin synchronous dive behaviour, however they drop in frequency when compared to carouselling, and both the percentage of initiator and solo dives increase. During dolphins' synchronous dives, foraging pods of dolphins plunge to deeper depths and push the corralled ball of fish to the surface (Neumann & Orams, 2003). While the ball of fish is still dense enough to allow for the formation of synchronous gannet dives, they do not last as long and are not as stationary as carouselled bait-balls, as the fish scatter at the surface. As a result, there is not enough time for prolonged gannet synchronous diving bouts to occur, and more numerous, shorter bouts take place, as

multiple initiators dive on fish scattering in groups at the surface. Solo dives increase, as individual fish are selected for individual capture.

Finally, the percentage of follower dives was lowest during dolphin line-abreast behaviour. This was also the only dolphin behaviour in which there were more solo gannet dives than follower dives. During this strategy, dolphins form a line and drive fish in a herd in front of them. While the fish may be densely packed, they are rapidly moving laterally to avoid the pursuing dolphins. This decreases gannets' ability to form long synchronous dive chains, as prey does not remain densely packed in stationary position long enough.

While the correlation between dolphin foraging behaviours and gannet synchronous dive behaviours were all associated with low statistical significance, the trends support the hypothesis that gannet synchrony is likely opportunistic, wherein the longest synchronous diving bouts take place when prey density is greatest for the longest duration.

5.6.4 Bryde's Whale Influence on Synchronous Diving Bout Formation

The presence of foraging Bryde's whales at MSFA's was associated with a statistically insignificant, but notable decline in the percentage of synchronous diving bouts. Like their influence on gannet dive mechanics, this is most likely a result of their scattering bait-balls on approach to lunge feed (Wiseman, 2008).

5.6.5 Hetero-specific Seabird Presence Influence on Synchronous Diving Bout Formation

Terns were the only hetero-specific avian species to be associated with a statistically significant decrease in both initiator and follower diving rates. Terns were also the only hetero-specifics not to be associated with any influence of dive mechanic variations, so it possible that any correlation between tern presence and gannet dive synchrony is coincidental. However, if gannets white plumage is developed to aid in triggering synchronisation (Forsman et al. 2002; Silverman et al. 2004; Seppänen et al. 2007), than it is possible the white colouration of terns may hinder the formation of synchronous diving bouts by sending false or conflicting signals. It was determined that the presence of petrel species was associated with the greatest relative increase in both initiator and follower dive rates. This may be a coincidental result of petrels being present, and more numerous at larger MSFA's. Shearwater species had the least effect on the rate of synchronous dives, with gannet initiator and follower dive rates remaining unchanged in their presence.

5.7 Conclusions

5.7.1 Plunge Diving

Relationships between dive heights and angles are consistent with earlier findings, wherein higher dive initiations were associated with a more vertical dive profile. Dive initiations themselves were correlated with a high percentage of dive completions. This suggests gannets select their dive profiles prior to initiation, and are largely committed to the energy expenditure associated with the dive and

subsequent take-off. Additionally gannet dive initiations may act as a form of local enhancement to conspecifics , as it is likely indicative of high probabilities of prey capture. Plunge diving behaviour was shown to be largely unaffected by tested weather parameters, however increased wind speeds decreased gannets ability to dive from height. This is thought to be a result of a decreasing ability to locate deeper prey sources as increasing winds intensify disturbances on the waters surface.

5.7.2 MSFA's

The hypothesis that foraging common dolphins increase the frequency of V-shaped gannet dive profiles by corralling fish to the surface was rejected, as the findings herein suggest that gannets are more likely to dive from height, and at steeper angles when foraging in association with common dolphins. This is thought to be because gannets appear to prefer taking dives based on prey density rather than depth. Choosing U-shaped dives into dense fish aggregations, where prey capture is more likely, rather than V-shaped ones at the surface where energy expenditure is decreased. Additionally, common dolphin foraging behaviours were found to act as indirect gannet dive initiation cues. Gannets were found to take the highest percentage of dives in response to dolphin carouselling behaviour, as fish are kept stationary and densely packed at the waters surface. Furthermore dive profiles varied accordingly with other dolphin behaviours, wherein gannets increased the percentage of V-shaped dives during common dolphin synchronous dives when fish were less densely corralled. This lends evidence to support the hypothesis that

gannets may adapt plunge diving behaviour in response to common dolphin foraging behaviour.

Finally, the impact of foraging Bryde's whales was shown to be minimal, however trends suggest that Bryde's whale presence may be associated with decreased gannet synchronous diving behaviour. More work, may however, be necessary to support this conclusion. Finally the presence of some con-specific seabirds is shown to decrease the altitude of gannet dives, as increased competition as increased surface predator presence was shown to hinder diving ability.

5.7.3 Dive Synchrony

Gannet plunge dive synchrony events were shown to likely be a result of local enhancement on the basis of prey density. Flocks of increasing size were shown to be one of the main influences in the formation of synchronous diving bouts, as increasing numbers of birds at more profitable MSFA's was associated with more frequent initiators, and followers. The formation of these bouts appeared to be based largely on the hetero-specific dive cues of wherein initiators favoured diving into dense prey assemblages, which were subsequently likely to provide a food source for followers. This was at least partially indirectly related to hetero-specific behaviours, as gannet synchrony increased during common dolphin foraging behaviours that most densely corralled fish. The size of foraging dolphin pods however was not shown to have as strong an effect on synchrony as gannet flock size, however synchrony rates did increase with the number of foraging dolphins.

5.8 Study Limitations

It is important to note that while the data collection in this study was extensive, it was subject to numerous limitations and constraints. The primary constraint within this study was the inability to gather subsurface video. Filming from such a large platform posed a number of constraints regarding the feasibility of subsurface data collection. Included in these was the inability to get close enough to work ups for them to be visible in underwater film before they dissipated. Additionally the logistical problems associated with obtaining underwater footage from a moving platform the size of *Dolphin Explorer* proved extensive. The use of a commercial vessel as the sole filming platform also limited the observations to the same diel scale, and as such, all data was collected during the mid to early afternoon. Previous studies on the effect of commercial whale watching vessels on dolphin pods found that dolphin behaviours were influenced by the vessels presence (Stockin et al. 2008b). As such, the filming platform itself likely influenced feeding events, by altering the behaviour of some observed foraging pods. The durations of feeding events may have been shortened, as fish would sometimes seek shelter below the vessel, or dolphins would break off feeding to socialise or investigate the vessel on approach. These factors therefore, may have skewed observations regarding the number of dives, or durations of behaviours that may otherwise have continued uninterrupted, or unimpeded.

There were also extensive difficulties in tracking and quantifying the influence of Bryde's whales within the study. It is difficult to accurately determine the location of Bryde's whales until they surface. As such they're subsurface

interactions with the feeding aggregation can often only be guessed at from where they break the surface.

The data collected over the course of this project was also skewed heavily to the autumn and winter months. As such, MSFA formation may be more heavily influenced by behaviours that are more commonly observed during winter months.

Despite the limitations of this study, this is, to my knowledge, the most extensive analysis of the above surface dive mechanics of both individual gannets, and collective synchronous behaviours of foraging gannet flocks. Information gleaned from this study adds to the growing wealth of knowledge on an important and unique marine predator, its social and foraging ecology, as well as how MSFA's are utilised, and what role they play in a broader ecological context within the gulf.

5.9 Future Research

Future research on gannet dive behaviour, especially in relation to MSFA's should aim to focus on the collection of subsurface video. The combined collection of subsurface video would allow for several knowledge gaps to be filled in regards to the influence of MSFA's on gannet dive behaviours. Namely, the depths and densities of bait-balls, as well as the specific behaviours of dolphins below the water could be more accurately assessed.

Additionally, the underwater behaviours of gannets could be linked to their above water dives, providing a more comprehensive picture of a complete gannet dive, and its influence both above and below the water. This valuable information

could help us to unravel questions on whether gannet's underwater paths influence the dives of follower gannets.

Finally, the collection of underwater footage would allow for an examination of how prey type may influence MSFA's as well as gannet behaviour. As prey is captured below the surface, it is difficult to gain data on prey type from above the surface. Both the size and species of targeted prey may prove an important factor in dive mechanics of MSFA formations in general. Additionally, information on whether synchrony increases prey capture success can be gathered.

As Bryde's whales movements are difficult to predict, and as they are often quite distant from work ups and may not be filmable even with below surface cameras, it may be advantageous to track them via aerial drones, as such methods are a well-proven tactic (George et al. 2004; Andriolo et al. 2006). The utilisation of an unmanned aerial vehicle in conjunction with below water footage at the site of work ups, could provide the most complete and comprehensive data set on marine MSFA's to date.

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