Feeding ecology of southern right whales (*Eubalaena australis*) on the South African west coast

by

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SUMMARY

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Abstract

South African southern right whales (*Eubalaena australis*, right whales) migrate between their low latitude calving grounds and their high latitude feeding grounds every year. In addition to these high latitude feeding grounds, right whales also feed on the South African west coast, specifically within a vigorously productive upwelling system (the Southern Benguela Upwelling System, SBUS). However, the feeding ecology of right whales here remain unknown, leading to the aims of the current study which, firstly, determined the sex and age class of individuals present on the west coast. Results indicated the presence of mostly female adults with an associated calf, which alluded to the west coast as a potential opportunity to build up energy reserves prior to migration. Secondly, prey hauls were conducted near presumed feeding right whales, as well as in a line of stations to determine targeted prey. Results indicated that right whales targeted mainly *Calanoides*, a large calanoid copepod that dominates copepod communities within the SBUS. Thirdly, both qualitative and quantitative behavioural data were used to assess right whale feeding behaviour. Qualitative data were available from behavioural observations done in 2003 – 2009, as well as in the current study. Results indicated that right whales were diving to feed at depth in the current study, compared to more frequent surface feeding observed previously, which could suggest a shift in the distribution of dense prey patches from shallower to deeper waters. However, a small sample size limited any firm conclusions. For the first time, quantitative behavioural data were collected by using animal-borne biologging tags, which measured the depth, pitch, roll, speed and heading of right whales during feeding. Results showed that right whales had comparable feeding bout duration and speed to other baleen whales in their feeding grounds. Also, right whales seem to maximize prey uptake by increasing foraging time at depth; well as in shallower waters by increasing foraging speed. This study represents the first steps into quantitatively investigating right whale feeding behaviour in a low latitude feeding ground.

LIST OF ABBREVIATIONS

BCLME	Benguela Current Large Marine Ecosystem
EBUS	Eastern Boundary Upwelling System
HBW	Humpback whale
NARW	North Atlantic right whale
SBUS	Southern Benguela Upwelling System
SST	Sea surface temperature

DECLARATION

I, Meghan Calista van Zyl, declare that the dissertation/thesis, which I hereby submit for the degree of Master of Science (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

ETHICS STATEMENT

I, Meghan Calista van Zyl, have obtained, for the research described in this work, the applicable research ethics approval, and declare that the research described in this work has observed the ethical standards required in terms of the University of Pretoria's Code of Ethics for Researchers and the Policy guidelines for responsible research.

Meghan Calista van Zyl
October 2023

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CHAPTER 1 LITERATURE REVIEW

1. SOUTHERN RIGHT WHALES

1.1 WHALING

Southern right whales (*Eubalaena australis*, right whales) earned their common name from English whalers, who believed that they are the ideal ("right") whale to hunt, since they swim slowly near the shore, float when dead and yield significant amounts of oil and baleen (Allen 1916; Best 2007). The coastal distribution of right whales is also very predictable (Best 2000) which made it especially easy for bay whalers to hunt them at their arrival to the coast every year (Richards and Du Pasquier 1989). Best (1970) summarised whaling in four steps: discovery, rapid acceleration of profitable fishing, over-exploitation, and collapse. The right whale hunting of the 18th and 19th-centuries followed the same path, and by the early 20th-century the global population was reduced to approximately 300 individuals (Best *et al.* 2001a). The three ocean basins of the Southern Hemisphere (South Atlantic, Indian Ocean and South Pacific) were once home to around 70 000 right whales (IWC 2001). However, this number is likely underestimated, as between the 18th and 20th-century approximately 97 700 right whales were killed by whalers (Best *et al.* 2001a; IWC 2001). Regardless, the extensive hunting of these whales brought the global population of right whales close to extinction (Dawbin 1986; Du Pasquier 1986). Indeed, only 60 mature females may have been left globally after 19th-century whaling, as suggested by population models (IWC 2001). Fortunately, a ban of right whale commercial whaling was implemented in 1935 by the International Convention for the Regulation of Whaling (IWC 2001). However, the recovery of right whales was further delayed by illegal Soviet whaling, which continued until the 1960s (Brownell *et al.* 2001; Clapham *et al.* 2004) and resulted in the loss of around 3 350 whales (Tormosov *et al.* 1998). As a result, the population would only reach its pre-Soviet catch numbers after again 18 years (Tormosov *et al.* 1998). Since the halt of any form of whaling on the species, right whale populations have been recovering from past over-exploitation (IWC 2001), with populations in Argentina/Brazil, Australia/New-Zealand and South Africa all displaying evidence of strong recovery (Cooke *et al.* 2001; Groch *et al.* 2005; Bannister 2009; Carroll *et al.* 2013; Brandão *et al.* 2018). However, the global populations of right whales still have a long way to go before they reach their historic pre-exploitation numbers (Jackson *et al.* 2008) and distributions (Richards 2009).

Figure 1. Photograph of a southern right whale swimming underneath the Mammal Research Institute Whale Unit's research vessel (which is 6m long) (© MRI Whale Unit).

1.1.1 Whaling in South Africa

Colonists on the South African coast were enthusiastic about starting a whaling industry, and they had reason to, because when van Riebeeck arrived in Table Bay in 1652, he noted "many thousands" of whales in the area, as well as in Saldanha Bay (Best 1970). However, the industry was not yet fully in swing, and whales were practically unexploited until the late 18th-century. Then, from the early 19th-century onwards, a noticeable plunge in the annual catch appeared in records from shore-based whaling (Best 1970). Therefore, 64 years after its discovery, the whaling industry in South Africa had over-exploited the right whale population, leading to a population "crash" (Best 1970). Nonetheless, despite the limited number of individuals, whaling pressure continued throughout the rest of the 19th-century to the early 20th-century, with only 18 whales killed over approximately 88 years (Best 1970). Then, by the early 20th-century, less than 100 individuals were caught annually in South Africa (Best 1970). By comparing this number to an estimated 12 000 whales killed across the entire South African coast between the late 18th and early 19th-century (Richards and Du Pasquier 1989), it is clear just how low the number of individuals were within the South African population just before the species was given international protection in 1935. Butterworth and Best (1990) estimated that by then there were between 10 – 29 adult females left in the South African population.

1.1.2 Whaling on the South African west coast

In the late 18th-century, American and British whalers came to chase right whales in Walvis Bay and Saldanha Bay (Figure 2) while getting water and supplies (Booth 1964). These whalers were very successful, for example, in St Helena Bay, 38 American ships took full cargoes of oil, and approximately 400 whales were caught in one season alone (Best 2006). Another strong example is the whaling success of 1790, when whalers killed so many whales in St Helena Bay, they simply harvested their baleen plates and let the carcass with its blubber float off (Theal 1900). Due to the success of these whalers, whaling in St Helena Bay, Saldanha Bay and Table Bay (collectively: the Cape of Good Hope, Figure 2) became an established whaling industry (Best 1970). Also looking for success, French whalers followed two years after the Americans and the Brits (Richards and Du Pasquier 1989), and killed right whales off the Cape of Good Hope during summer months (Best 2006). However, French whalers started to lose interest in exploiting the South African west coast in favour of the Namibian coast, and largely abandoned St Helena Bay by 1792 (Best 2006). In addition, British whalers moved their operations away from the South African west coast to Walvis Bay (Best 2006). Therefore, whaling at the Cape of Good Hope (and specifically St Helena Bay) was a flash in the pan (Best 2006). Although brief, this west coast whaling industry resulted in the harvesting of an estimated 1 484 right whales in about 6 years (Best 2006).

While other whaling industries had caught the most whales in winter/early spring (Best and Ross 1896), historical records indicated a different catching pattern at the Cape of Good Hope. Here, whales were taken earlier and later in the year (i.e. during summer months) as compared to whaling grounds in Mozambique and Namibia, where there was a winter/early spring whaling season (Richards and Du Pasquier 1989).

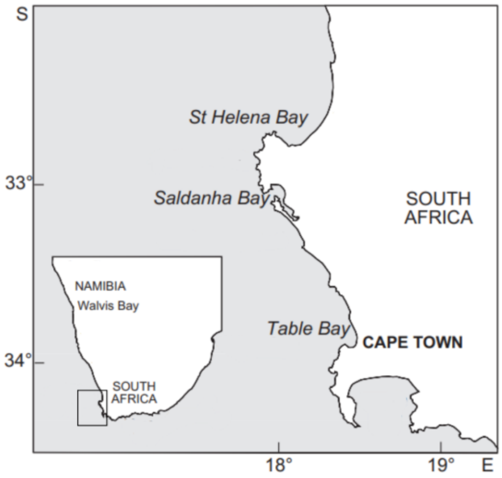

Figure 2. Established right whale whaling grounds of the late 18th-century in St Helena Bay, Saldanha Bay and Table Bay (collectively: the Cape of Good Hope) as well as the Walvis Bay whaling ground in Namibia. The rectangle in the bottom left shows the position of the Cape of Good Hope on the greater southern African west coast. Adapted from (Best 2006).

1.2 DEMOGRAPHICS AND RECOVERY

Whaling between the 18th and early 20th-centuries resulted in the loss of an estimated 48 000 right whales in the South Atlantic, 37 200 in the South Pacific and 12 500 in the Indian Ocean (Dawbin 1986; Du Pasquier 1986; Best 1987). A first global population estimate indicated roughly 13 600 right whales occupied the Southern Hemisphere in 2009 (IWC 2013). However, the global population of right whales have not reached its pre-exploitation levels (Jackson *et al.* 2008) and the population is estimated at < 13.0% of its carrying capacity (Tulloch *et al.* 2018).

It is not surprising that their road to recovery will take some time as right whales are long-lived (Burnell 2001; Charlton 2017). Another contributor to their long recovery is the amalgamation of extreme whaling pressure and a slow reproductive rate (Tulloch *et al.* 2018). Female right whales give birth to one calf every three years (Knowlton *et al.* 1994; Best *et al.* 2001b; Kraus *et al.* 2007) and this 3-year calving interval includes one year of gestation, one year of lactation and another to rest (Payne 1986; Best *et al.* 2001b; Cooke *et al.* 2001). One study estimated that, even if there are no right whales caught for 100 years, the population will still be at < 11.0% of its carrying capacity (Tulloch *et al.* 2018).

Despite the depletion caused by whaling, right whale populations in Argentina/Brazil, Australia/New-Zealand and South Africa all have evidence of strong recovery (Cooke *et al.* 2001; Groch *et al.* 2005; Bannister 2009; Carroll *et al.* 2013; Brandão *et al.* 2018). However, right whales show little evidence of recovery in historic calving grounds of Chile/Peru, Southeast Australia, Tristan Da Cunha, Mozambique/Madagascar, and Namibia (IWC 2001; Best *et al.* 2009; Galletti Vernazzani *et al.* 2014; Carroll *et al.* 2015; Roux *et al.* 2015).

The Southwest Atlantic has two important calving areas in Argentina (Península Valdés) and Brazil (Santa Catarina) (Payne 1986; Payne *et al.* 1990; Rowntree *et al.* 2001). The population calving off Península Valdés was estimated to have an annual increase rate of 6.0% between 1979 – 2010, and recently was estimated to consist of around 4 007 individuals (IWC 2013; Jackson *et al.* 2021). The Brazilian Right Whale Catalogue had 315 individuals identified in 2003, with an annual increase rate of 29.8% for reproductive females from 1997 – 2003 (Groch *et al.* 2005). However, this increase rate did not fall within the range of biologically plausible rates of increase for right whales (Best *et al.* 2001b). Therefore, it was most directly attributed to immigration from individuals of the Península Valdés calving ground, although shifts in right whale distribution and increased survey efforts could also have played a role (Groch *et al.* 2005).

Based on genetic diversity, as well as differing population growth rates, the Australian population is divided into two subpopulations, one in southeast and the other in southwest Australia (Bannister *et al.* 2011; Carroll *et al.* 2015, 2019). Based on aerial survey data of 1993 – 2015, the southwestern subpopulation has around 3 191 individuals (Smith *et al.* 2019) with an increase rate of 6.2% per year (Bannister 2018). In contrast, the southeastern subpopulation was estimated to have around 257 individuals (Watson *et al.* 2013; Bannister 2018) and, recently, Stamation *et al.* (2020) found that this population is increasing at 4.7% per year. Despite being reduced to a small remnant population at Campbell Island after 19th and 20th-century whaling (Richards 2002, 2009; Jackson *et al.* 2008), the New-Zealand population has been recovering since the species' international protection with an estimated 908 individuals within the population in 1998 (Carroll *et al.* 2011b). In addition, the population had an increase rate of 4.8% between 2006 – 2016 (Davidson *et al.* 2016).

South African right whales come to the south coast calving grounds in late June to late October, with peak calving in August (Best 1994). Since 1971, this population has been monitored through annual coastal aerial surveys (Best 1990, 2000). These long term monitoring data have also revealed a drastic decrease in the coastal presence of non-calving adults, and a reduction in the population calving rate since 2009 (Vermeulen *et al.* 2019). Specifically, there has been an increase in the calving intervals from 3 years, to 4- and 5-year intervals (Vermeulen *et al.* 2019). These extended calving intervals could be the result of early abortions, or late-term abortions/loss of neonates, as was suggested to be the case for a closely related species, the North Atlantic right whale (*Eubalaena glacialis*, NARW) (Knowlton *et al.* 1994). Consequently, the population growth rate has declined from 7.1% per year (Best *et al.* 2001b) to 6.5% per year (Brandão *et al.* 2018) and recently, the population was estimated to have around 6 470 individuals (Brandão *et al.* 2023).

1.3 DISTRIBUTION

1.3.1 Global

Townsend (1935) created a map which plots “the position of each whaleship on a day when one or more right whales were taken.” This map shows, firstly, the broadscale patterns where right whales were seen and killed. Right whales were particularly concentrated in a great band, stretching from east of Tristan da Cunha towards the Cape of Good Hope, and from 30°S to 40°S (Townsend 1935, Figure 3). In his review, Richards (2009) used Townsend’s map, as well as other historical records and found that right whales were seen east of Madagascar, off Brazil, and western Australia, as well as in southern Mozambique.

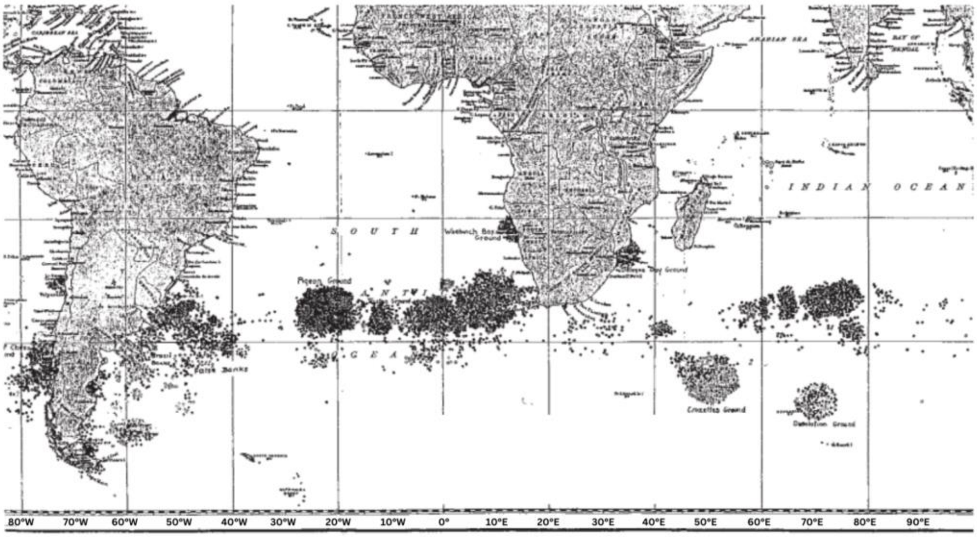

Figure 3. Locations of right whale kills in the South Atlantic and Indian Oceans. Adapted from Townsend (1935).

Whalers meticulously combed through the oceans in search of whales; so, secondly, Townsend’s map could also be an indication of where right whales were not seen (Townsend 1935; Richards 2009). One area that seems to be devoid of whales is the “ocean desert”, a huge expanse of 5 000km east-west and north-south between 142°W and 80°W where only four whales were captured (Figure 4). This is described by Richards (2009) as the “evidence of absence.” Although the whalers were driven to find whales, they could not withstand the harsh conditions south of around 45°S, and as a result, Townsend’s map lacks a substantial number of catches made south of 50°S (Tormosov *et al.* 1998). In fact, right whales were caught during illegal soviet whaling as far south as 64°S (Tormosov *et al.* 1998).

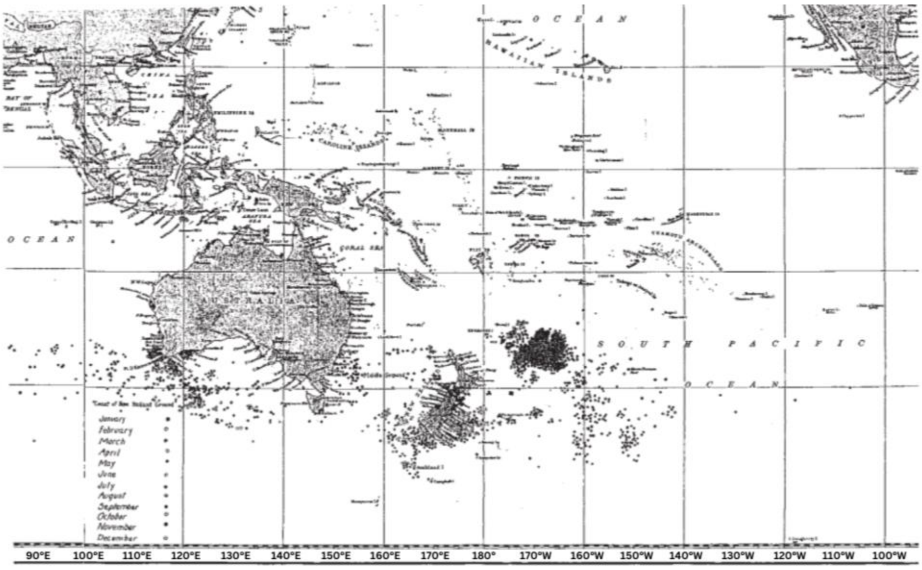

Figure 4. Locations of right whale kills in the Pacific Ocean. Richards (2009) described the area between 142°W and 80°W as the “ocean desert”, indicating the “evidence of absence” of right whales. Adapted from Townsend (1935).

Currently, at a much smaller global population size, the distribution of right whales extends from approximately 20°S to 55°S (Antarctic Convergence) (Best 2007), however, these limits are not absolute. For example, right whales venture further north into the west coast regions of South America and southern Africa, where cold currents extend into tropical waters (Best 2007). Some changes in the distribution of recovering populations have been recorded, for example, right whales are wintering in the Falkland Islands

(Weir and Stanworth 2019) and recolonising mainland New-Zealand (Carroll *et al.* 2014). These changes show that recovering populations may not mirror the distribution/connectivity patterns that were in place before exploitation occurred. These changes are also particularly evident when habitat use changed rapidly (Harcourt *et al.* 2019).

One factor of right whale distribution has not changed and that is that both female and male right whales have high fidelity to winter calving grounds (IWC 2001; Rowntree *et al.* 2001; Carroll *et al.* 2013) and summer feeding grounds (Best 2000; Valenzuela *et al.* 2009; Carroll *et al.* 2020). Right whales also migrate between these grounds every year (Cummings 1985). It is hypothesised that moving to calm water is an underlying reason for migration in right whales (Whitehead and Moore 1982; Corkeron and Connor 1999; Clapham 2001). The other hypotheses for baleen whale migration include optimising energy budgets for both females and calves (Brodie 1975) and reducing the predation risk of calves (Corkeron and Connor 1999).

1.3.2 Calving – and associated feeding grounds

Female right whales show a high degree of philopatry to natal calving grounds, and this preference to certain coastal nursery areas were thought to be because of certain environmental characteristics (Best 2000). The depth and water calmness, as well as the softness of substrate seems to be important environmental factors that determine the coastal distribution of right whales (Thomas 1987). The preference for calm waters can be two-fold, firstly, it allows the cow/calf pair to conserve their energy and invest this saved energy in growth and lactation. Secondly, calves struggle to surface and breathe in rough waters (Thomas and Taber 1984), meaning there is, especially for calves, a lesser chance of injury, and a greater chance of survival in calmer waters. In fact, Elwen and Best (2004a) found that 73% of the cow/calf pairs on the South African south coast congregate in bays that provide swell and wind protection. These bays also had sandy and gently sloping bottoms (Elwen and Best 2004a). Specifically, cow/calf pairs preferred sandy beaches over rocky shores (Elwen and Best 2004a), which may protect the calf from injury (because there is a lack of obstacles) (Elwen and Best 2004b). However, strong patterns in the distribution of whales on the South African coast suggests that calm water is the primary environmental factor that determines their choice of habitat at their calving grounds (Elwen and Best 2004a, b).

The text below will discuss the major calving grounds, and their associated feeding grounds, of the southwest Atlantic (Argentina, Brazil), Australia/New-Zealand, and the southeast Atlantic (South Africa). It is at these calving grounds that right whales have demonstrated the strongest recovery (Cooke *et al.* 2001; Groch *et al.* 2005; Bannister 2009; Carroll *et al.* 2013; Brandão *et al.* 2018). Other right whale calving grounds of the south central Atlantic (Tristan da Cunha/Gough Island), southwest Indian Ocean (Mozambique, Madagascar), and the southwest Pacific (Chile/Peru) will not be discussed in this review.

Southwest Atlantic

The majority of right whales in the southwest Atlantic spend their time between May and December on the calving grounds of Península Valdés (42°S – 43°S) and southern Brazil (27°S – 29°S) (Rowntree *et al.* 2001; Groch *et al.* 2003; Espírito Santo *et al.* 2009, Figure 5). However, solitary individuals, small groups and cow/calf pairs have also been seen outside of these calving grounds, for example in Cabo Vírgenes and Rio Negro Province (Failla *et al.* 2008, Figure 5), as well as outside of the main aggregation area in Brazil (Lodi and Tardelli Rodrigues 2007; Santos *et al.* 2010). In addition, while only a few cow/calf pairs have been seen along the coast of Uruguay (33°S – 35°S, Figure 5), solitary individuals and socially active groups are seen regularly (Costa *et al.* 2005, 2007)

Right whales in the southwest Atlantic have a broad feeding range, including historical offshore feeding grounds 30° − 45°S (Smith *et al.* 2012), the Patagonian Shelf (Rowntree *et al.* 2001, Figure 5) and the Scotia Sea (Moore *et al.* 1999; Reilly *et al.* 2004). By analysing stable carbon and nitrogen values within right whale skin, Valenzuela *et al.* (2018) suggested that whales which calve off the Argentinean coast use all three feeding areas. Records from 19th-century and modern whaling also indicate that these whales have feeding grounds at the Patagonian Shelf (IWC 2013). Other feeding grounds inferred, from the same records, are between 30°S – 55°S, and west of 40°W (or offshore Argentina, Uruguay, and southern Brazil) as well as the Falkland Islands and South Georgia (IWC 2013, Figure 5). Right whales have also been seen foraging for krill and isopods in Cabo Vírgenes, outside of the calving season (IWC 2013), and at their Península Valdés calving ground during calving season (Payne 1995; Sironi 2004; Hoffmeyer *et al.* 2010). However, it appears that the main feeding grounds of right whales in the southwest Atlantic is around South Georgia (Leaper *et al.* 2006).

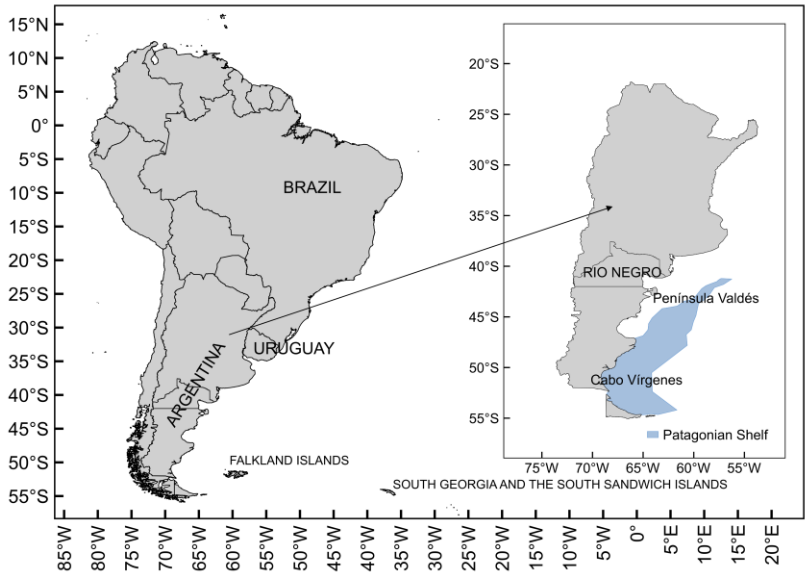

Figure 5. Map of South America indicating the most important calving area of Southwest Atlantic right whales (Península Valdés), as well as their feeding grounds (Patagonian Shelf, Falkland Islands and South Georgia).

Australia/New-Zealand

Aerial surveys conducted since 1976 indicated that right whales distribute as far north as Exmouth and Hervey Bay (Figure 6) on the west and east coast of Australia, respectively. However, during winter, most right whales can be seen between Cape Leeuwin (34°22'S, 115°08'E) in western Australia and Ceduna (32°08'S, 133°41'E) in south Australia (IWC 2013, Figure 6). However, like in the southeast Atlantic, individuals can be found outside of the major concentration areas. For example, right whales also occur, albeit in much smaller numbers, on the coast of Victoria, Tasmania, and New South Wales (IWC 2013, Figure 6). Of the 13 aggregation areas on the southern coastline of Australia, the Head of Bight (South Australia) is the most important right whale aggregation area (Figure 6). However, right whale numbers in Fowlers Bay, located 160km southeast of this area (Figure 6), has increased since 2004. Mothers with calves also use this habitat extensively (Charlton *et al.* 2019). Since the estimated rate of increase in Fowlers Bay exceeds the maximum rate for the species, right whales from other aggregation areas must be moving into

Fowlers Bay (Charlton *et al.* 2019). Indeed, when right whale abundance was high at Head of Bight, the abundance at Fowlers Bay would increase (Charlton *et al.* 2019). Therefore, it seems that when Head of Bight reaches "saturation capacity", individuals move to find suitable habitat at Fowlers Bay (Charlton 2017). Nevertheless, the Head of Bight remains the most important aggregation area of right whales on the Australian coast.

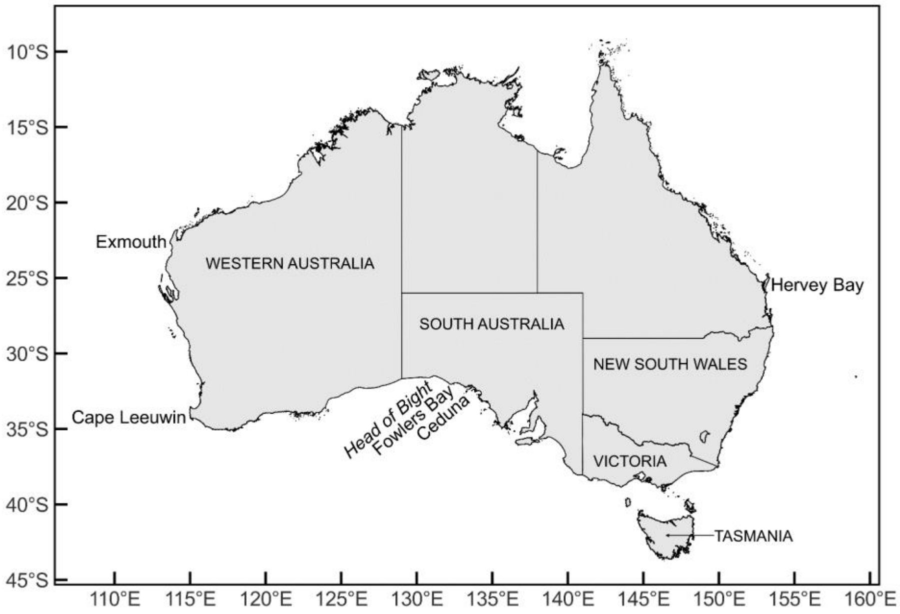

Figure 6. Map of Australia indicating areas of Australian right whale occurrence. These whales can be seen between Cape Leeuwin and Ceduna in winter months, with their main aggregation area being the Head of Bight.

The Australian population is genetically distinct and is recovering independently from the New-Zealand population (Baker *et al.* 1999; Patenaude *et al.* 2007), where right whales also visit during the austral winter, and females give birth and nurse calves (Richards 2002). Although a small number of right whales still winter at Campbell Island (Stewart and Todd 2001), as well as in mainland New-Zealand (Patenaude 2003; Carroll *et al.* 2011a), sub-Antarctic Auckland Islands (Figure 7) seem to be the main calving ground for right whales in New-Zealand (Patenaude *et al.* 1998; Patenaude and Baker 2001). Yearly surveys conducted between 1995 – 1998 (Patenaude *et al.* 1998; Patenaude and Baker 2001) and 2006 – 2009 (Childerhouse *et al.* 2009) showed that the northern end of Auckland Islands and Port Ross (Figure 7) make up the main right whale calving area in New-Zealand. Particularly, Port Ross has the highest concentration of right whales wintering in Auckland Island (Rayment *et al.* 2012). However, it is worth noting that Campbell Island has not been surveyed since 1997 (Stewart and Todd 2001). This might be due to the impossibility of systematically monitoring a population of right whales that is centred around a remote island (Best 1993). Although right whales winter in mainland New-Zealand and sub-Antarctic New-Zealand, these are not genetically distinct stocks (Carroll *et al.* 2011). The hypothesis is rather that the once extirpated mainland New-Zealand is being re-colonized by individuals from sub-Antarctic New-Zealand (Carroll *et al.* 2011a).

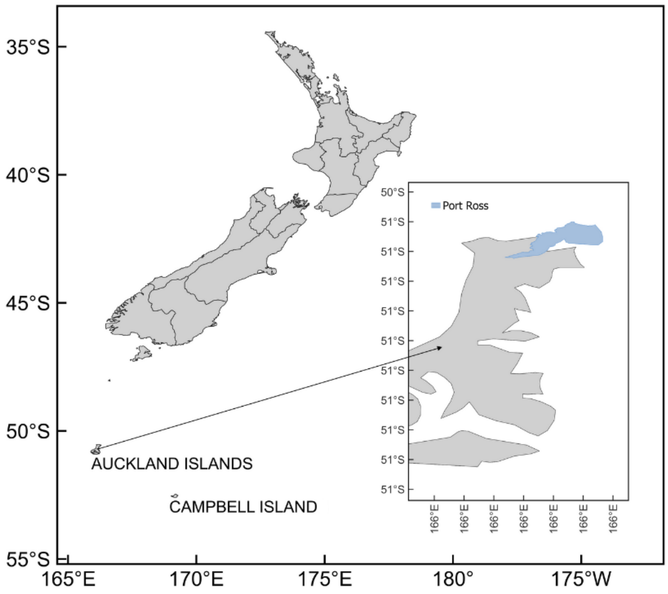

Figure 7. Map of New-Zealand indicating the calving areas for the New-Zealand population of right whales which include, mainland New-Zealand, Campbell Island, and the Auckland Islands (main calving area).

South Africa

The South African south coast is the primary calving ground for right whales in the southeast Atlantic (IWC 2013) and the population likely has important feeding grounds at the Subtropical Convergence, and the Polar Front (Mate *et al.* 2011), as well as off the coast of South Africa, and Bouvet Island (Best and Schell 1996; Mate *et al.* 2011). Right whales from the population also migrate east to west, from their calving grounds to their Gough Island feeding grounds (Best *et al.* 1993). Just as in Península Valdés, right whales engage in opportunistic feeding in their South African calving grounds (Best and Schell 1996). The South African west coast, and particularly St Helena Bay, is a known feeding ground for this population (IWC 2013).

Between 1979 – 2008, most right whales on the southern African coast were found between 18°30'S and 21°30'E (IWC 2013). However, due the focus on known nursery areas during the calving season, many aerial surveys occurred on the south coast (Best 2006). Although some surveys extended into the west coast, they are limited to September to October (Barendse and Best 2014), consequently, not much is known about the distribution and seasonal occurrence of right whales in the South African west coast (Barendse and Best 2014).

1.4 FEEDING

1.4.1 Feeding apparatus

Family Balaenidae comprises of four balaenid whales, including the bowhead whale (*Balaena mysticetus*) and three species of right whales (southern right whale (*Eubalaena australis*); North Atlantic right whale (*Eubalaena glacialis*); and the North Pacific right whale (*Eubalaena japonica*)). Along with Bowhead whales, right whales use baleen plates, which have filaments acting like a sieve, to capture prey equal to and larger than 0.3mm (Mayo *et al.* 2001; Diedrich 2013). They feed via continuous ram filter feeding (Baumgartner *et al.* 2007). A mode of filtering where, by swimming at a slow and steady pace, right whales push prey-filled water past their exposed baleen plates (Werth 2000). As right whales swim forward, water enters through a gap between two racks of baleen plates (subrostral gap) on either side of their mouth and exists continuously just in front of their eyes (Baumgartner *et al.* 2007). Not only can water flow unidirectionally through the mouth, but hydrodynamic conditions create mild suction in front of the mouth which improves filtering efficiency (Werth 2004). Therefore, it seems that the right whale body plan and baleen organization are well adapted to ram filter feeding (Woodward 2006; Baumgartner *et al.* 2007).

Commented [A1]: ?? Should be bowhead whale

Ram filter feeding appears to be the most energy efficient at slower swimming speed, as energy expenditure increases exponentially when right whales force their baleen plates through water at faster speeds (Baumgartner *et al.* 2007). Also, when right whales swim at slower speeds, water flows more optimally through their mouths and baleen plates (Hamner *et al.* 1988; Werth 2004). Therefore, the diet of right whales is restricted, firstly, as they can only successfully capture prey of a certain minimum size, due to the filtering efficiency of their baleen plates (Baumgartner *et al.* 2007). Secondly, only prey that swim slowly enough to be captured is available to right whales, as certain fast-swimming species are able to evade feeding right whales (Baumgartner *et al.* 2007).

Right whales rely on the environment to concentrate their prey into dense patches, and it is at their feeding grounds where temperature and ocean currents lends itself to the development of these prey quality and quantity (Baumgartner *et al.* 2007). Habitat models using 19th and 20th-century whaling data revealed that right whales also feed close to thermoclines and currents, which are oceanographic features that creates dense patches of prey (Torres *et al.* 2013; González Carman *et al.* 2019). However, these processes and prey production within their environment change across regions and years, leaving right whales to search for often unreliable, continuously moving, prey resources (Baumgartner *et al.* 2007). There is still uncertainty around how right whales locate prey resources over large scales, but some suggestions include echolocation or listening for prey noises (Hamner *et al.* 1988). Right whales may also just forage at random after returning to an area where they remember feeding successfully in the past (Hamner *et al.* 1988). Nevertheless, Hamner *et al.* (1988), observed a right whale swimming directly towards prey for an hour to feed on the patch below the surface. This demonstrates that right whales, like NARWs, can navigate directly to prey patches (Watkins and Schevill 1979). In fact, since baleen whales feed more successfully when their prey aggregates into dense patches, the distribution of feeding baleen whales is a useful indication of where there is oceanographic productivity (Moore *et al.* 2002; Friedlaender *et al.* 2006). In summary, right whales feed wherever there are dense patches of prey available, making them opportunistic feeders (Werth 2001) as well as specialist feeders, because they target prey of a certain size that swim slow enough to be captured (Kenney 2002).

1.4.2 Feeding behaviour

We have limited knowledge of right whale feeding behaviour, however, that which we know derives from whaling records in the 19th and 20th-centuries (IWC 2001), observing feeding near shore (Hamner *et al.* 1988), transect surveys in the Southern Ocean (Reilly *et al.* 2004) and satellite tagging (Mate *et al.* 2011; Zerbini *et al.* 2015; Best and Mate 2023).

Right whale ram filter feeding operates like a net when removing items from water; as a result, right whales are referred to as “skimmers” (Baumgartner *et al.* 2007; Werth and Potvin 2016). Although right whale feeding is mostly seen at the surface, they can filter feed throughout the water column (Werth and Potvin 2016). To follow the prey at all levels of the water column, right whales likely use tactile senses, in the form of sensory hairs around their mouths, which bend when they are struck by prey that are in close proximity

(Payne 1976; Baumgartner *et al.* 2007; Kenney *et al.* 2020). They can make these fine-scale movements, adjust vertically, and turn, to filter feed on the highest concentration of prey for several hours without interruption (Mayo and Marx 1990; Baumgartner *et al.* 2007)

Hamner *et al.* (1988), observed right whales feeding in the Antarctic Peninsula. When prey was at the surface, one whale skim-fed with its upper jaw lifted above the surface. However, when prey was below the surface, whales engaged in sub-surface feeding and dove repeatedly in place. Dive duration was short, and the time between dives and surface intervals were erratic when whales were feeding on small, scattered prey patches. However, dive duration was longer and the time between dives and surface intervals were more regular when whales were feeding on larger prey patches. At the large patch, successive dives also became shorter with time. Longer dives were preceded by hyperventilation, showing that the right whales anticipated the dives. One dive was followed with a right whale opening and closing its mouth at the surface, with baleen visible, which right whales seemingly do to separate captured prey from water before swallowing (Watkins and Schevill 1976).

1.4.3 Prey species

Right whales feed primarily on large quantities of zooplankton, including copepods, krill, pteropods or larval stages of other crustaceans (Cummings 1985; Baumgartner *et al.* 2007); as well as soft-bodied ctenophore prey (Bastida and Rodríguez 2003).

In the southwest Atlantic, right whales feed on copepods in lower latitudes (Valenzuela *et al.* 2009, 2018) for example, off the Patagonian shore (Payne *et al.* 1983). They also feed on Antarctic krill (*Euphausia superba*) in higher latitudes for example South Georgia, the Scotia Arc, and the South Sandwich Islands (Valenzuela *et al.* 2009, 2018). This latitudinal change in the prey species is also reflected in Soviet whaling records, which show that the stomach contents of right whales taken north of 40°S contained 94% copepods (Tormosov *et al.* 1998), whereas south of 50°S, right whales targeted krill (Tormosov *et al.* 1998). Right whales also feed on krill in the Antarctic Peninsula (Matthews 1932; Hamner *et al.* 1988) and rely on krill as their main food source in the Southern Ocean (Laws 1985).

1.4.4 Zooplankton

Zooplankton, like copepods and krill, feed on primary producers (phytoplankton) and transfer this energy to higher trophic organisms in marine food webs (Kiørboe 1993; Lenz 2000).

Copepods

Copepods feed on detritus, small heterotrophs, and phytoplankton (van Duren and Videler 1996). In turn, fish, larger zooplankton, and marine mammals (like right whales) feed on copepods (Mauchline 1998; Lenz

2000; Hoffmeyer *et al.* 2010; Leandro *et al.* 2010; Baumgartner *et al.* 2013; D'Agostino *et al.* 2016). External and internal factors influence the fecundity of copepod species, which also depends on the space and time in which copepods are producing eggs (Armstrong *et al.* 1991). Some of these factors include body size, sea surface temperature, and food availability (Armstrong *et al.* 1991).

Four to five copepod species typically dominate the copepod assemblages in upwelling areas, making up more than 80% of the zooplankton biomass (Peterson 1998). One of these species is *Calanoides carinatus*, a copepod which inhabits all upwelling systems of Africa (Verheye 1991). *C. carinatus* has fast development and high egg production rates which enables it to rapidly increase in abundance during upwelling events (Borchers and Hutchings 1986; Peterson and Painting 1990). In addition, when food conditions improve, female *C. carinatus* recover rapidly after they stopped producing eggs when food conditions were weak (Huggett 2001). Adults and copepodites of *C. carinatus* can overcome extensive periods of starvation between upwelling events because they have the largest lipid reserves of all calanoid copepods (Borchers and Hutchings 1986; Armstrong *et al.* 1991).

Krill (euphausiids)

The biomass of Antarctic krill is strongly associated with physical processes in the Southern Ocean, especially the extent and duration of sea-ice (Loeb *et al.* 1997). Warmer sea surface temperatures (SST) have a negative impact on krill recruitment (Murphy *et al.* 2007), in fact increased SST during El Niño events, which reduces the sea ice extent, affects the krill abundance in following years (Trathan and Murphy 2003; Nicol *et al.* 2008). For example, the krill abundance in South Georgia declined during El Niño events, when the SST was higher than normal (Trathan *et al.* 2006). Indeed, krill species have been affected by SST warming (Atkinson *et al.* 2004; Kawaguchi *et al.* 2011).

1.4.5 Feeding and reproductive success

Changes in oceanographic conditions in the Southern Ocean and global climate change signals influence right whale population dynamics and breeding success (Leaper *et al.* 2006; Seyboth *et al.* 2016). Moreover, as specialist feeders, that target prey of a specific size and mobility, right whales are especially vulnerable to global climate change impacts, as reproductive variability is induced by changes in their environment, mediated through feeding success (Greene and Pershing 2004). As capital breeders, right whales use the energy they gain in their feeding grounds to reproduce (Jönsson 1997); therefore, their breeding success is strongly related to their feeding success (Leaper *et al.* 2006; Lockyer 2007; Seyboth *et al.* 2016). Nutrition is vital to successful conception, gestation, and lactation (Reeves *et al.* 2001; Berta *et al.* 2005) and nutritional stress has been linked to a lowered reproductive output in cetaceans (Lockyer 1986; Reeves *et al.* 2001; Greene *et al.* 2003; Hlista *et al.* 2009; Ward *et al.* 2009; Williams *et al.* 2013). Moreover, sufficient food resources are vital to the adequate storage of energy as fat reserves, which seems to be necessary for right whales to reproduce successfully (Miller *et al.* 2011). It was also suggested that the number of calves produced by right whales in Brazil is negatively affected by krill density (Seyboth *et al.* 2016).

A recent study has revealed changes in the feeding strategy of the South African right whale population; as well as a shift of its feeding efforts equatorward (van den Berg *et al.* 2021). In addition, these changes coincide with a period of slowed population growth (Brandão *et al.* 2018) and an increase in calving intervals (Vermeulen *et al.* 2019). Since right whales rely on dense patches of zooplankton to feed successfully (Wishner *et al.* 1995), these changes may indicate environmental change in the feeding grounds of the population.

2 UPWELLING ON THE SOUTH AFRICAN WEST COAST

2.1 EASTERN BOUNDARY UPWELLING SYSTEMS

Eastern Boundary Upwelling Systems (EBUSs) are found along the edges of eastern boundary currents in both the Pacific and Atlantic Oceans. Here, at these major upwelling zones, alongshore winds force surface waters offshore which is replaced with cold, nutrient-rich water from depth (termed Ekman transport) (Wooster and Reid 1963; Sverdrup 1983; Wang *et al.* 2015). This upwelling of deeper waters to the euphotic zone brings nutrients to phytoplankton for use during photosynthesis, resulting in phytoplankton blooms. As a result, EBUSs are some of the most vigorously productive marine ecosystems in the world (Cushing 1969; Ryther 1969). In fact, while EBUSs only cover around 2% of the ocean surface, they are responsible for 7% of the primary production in marine ecosystems globally (Pauly and Christensen 1995). The primary production in EBUSs provide nourishment for zooplankton communities, that then link this primary productivity to predators like seabirds, marine mammals, and other pelagic fish (Cury *et al.* 2000; Roy *et al.* 2001). In addition EBUSs modulate global climates (IPCC 2014).

2.1.1 Benguela Current Large Marine Ecosystem

There are four major EBUSs globally: the Canary Current (South America), the California Current (North America), the Humboldt Current (northwestern Africa), and the Benguela Current Large Marine Ecosystem (BCLME) off southwestern Africa (Hill *et al.* 1998). The BCLME spans from 5°S, 12°E off the Angolan coast to 34°S, 26°E south of Cape Point (Lutjeharms and Stockton 1987) and supports key fisheries in Angola, Namibia and South Africa. This system shares characteristics with the other EBUSs, however, uniquely, it is bounded by the warm Angola Current on its northern extremity, and by the warm Agulhas Current on its southern extremity (Shannon and Nelson 1996; Shillington 1998; Shannon and O'Toole 2003, Figure 8).

Ekman transport, as well as cyclonic curl of the wind stress (Rykaczewski and Checkley 2008) are two mechanisms that result in upwelling. Although curl-driven upwelling is responsible for 23% of the upwelled waters in the Benguela (Messié *et al.* 2009), Ekman transport seems to be more vital to ecosystem functioning as it upwells deeper and more nutrient-rich waters to the euphotic zone (Chavez and Messié 2009). The most intense upwelling occurs at Lüderitz, Namibia (Figure 8) (Hardman-Mountford *et al.* 2003). This upwelling area creates a partial environmental barrier that separates the BCLME into two subsystems (northern Benguela, and southern Benguela) that have different physical and biological characteristics (Hutchings *et al.* 2009). Specifically, water in the southern Benguela, or Southern Benguela Upwelling System (SBUS), is more oxygenated and less saline than in the northern Benguela (Hutchings *et al.* 2009). In addition, pelagic fish populations, as well as a few phytoplankton and zooplankton species are different in the northern Benguela compared to the SBUS (Lett *et al.* 2007). Also, while the northern Benguela has year-round upwelling (on average 95% of the year), upwelling in the SBUS is strongly seasonal and occurs for 75% of the year (Verheye *et al.* 2016; Lamont *et al.* 2018).

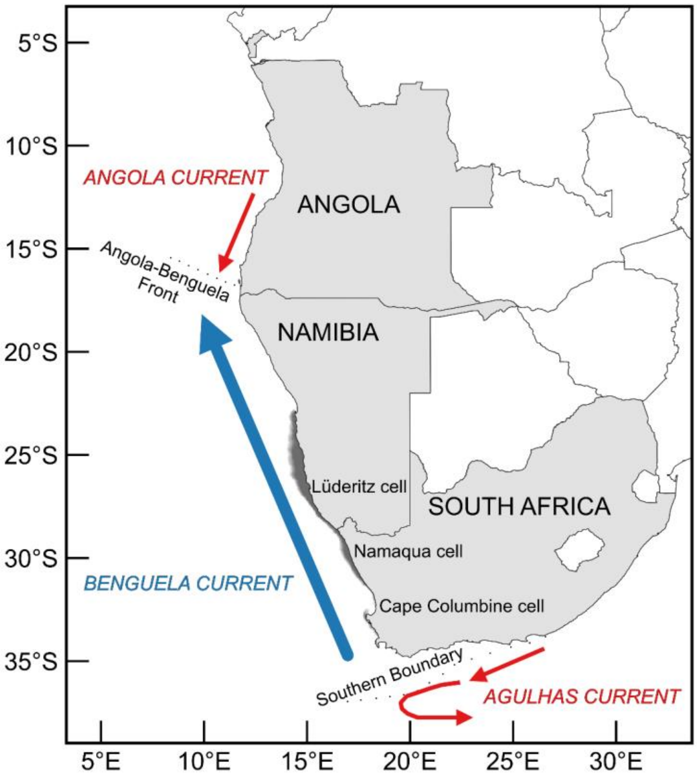

Figure 8. Map showing the location of the Benguela Current Large Marine Ecosystem, bounded by the warm Angola Current to the north, and the Agulhas Current to the south. The discrete upwelling cells are also indicated with grey shading (Cape Columbine, Namaqua, and Lüderitz).

2.1.2 The Southern Benguela Upwelling System

The SBUS borders the northern Benguela upwelling area off Lüderitz to the north, and the Agulhas current to the south and east (Huggett *et al.* 2009, Figure 8). There are distinct wind-driven coastal upwelling areas within the subsystem (Verheye *et al.* 2016) where south-easterly, upwelling-favourable winds peak in summer and autumn (Hutchings *et al.* 2009). Shannon and Nelson (1996) defined these upwelling areas (from north to south): the Namaqua cell (from 29°S to 31°S), the Columbine cell (from 31°S to Cape Columbine), the Cape Peninsula cell (from Cape Columbine to Cape Point) and the Western Agulhas Bank (from Cape Point to Cape Agulhas). High primary productivity is associated with wind-driven upwelling (Huggett *et al.* 2009), thus these upwelling areas have elevated chlorophyll index values during the summer (Jarre *et al.* 2015). However, zooplankton production differs between upwelling areas. For example, the copepod biomass and production was significantly higher off Cape Columbine and Namaqua upwelling areas, compared to Cape Peninsula upwelling area between 1988 – 2003 (Huggett *et al.* 2009). In fact, the Namaqua and Cape Columbine cells are the most active upwelling areas in the SBUS (Demarcq *et al.* 2003). Copepod biomass were also significantly higher in summer compared to winter during the same period (Huggett *et al.* 2009). Therefore, upwelling does occur during the winter, although it is significantly reduced (Huggett *et al.* 2009). Zooplankton abundance and copepod densities are particularly high north of Cape Columbine, especially in the retentive environment of St Helena Bay (Verheye *et al.* 1992) where the oceanography lends itself to pulsed seasonal upwelling from October to March (Shannon 1985; Hutchings *et al.* 2009).

The zooplankton abundance in the SBUS increased significantly between 1951 – 1996 (Verheye *et al.* 1998), and it was suggested that this was due to a decrease in predation pressure of sardines and anchovy and an intensification of upwelling in the region (Verheye *et al.* 1998). This intensification has continued as the total cumulative upwelling, and number of days upwelling occurred was still increased linearly, although not significantly, within the SBUS between 1979 – 2014 (Lamont *et al.* 2018). Other changes over the past 20 years include changes in SST and increases in the number of extreme events and harmful algal blooms (Rouault *et al.* 2010; van der Lingen *et al.* 2016; Lamont *et al.* 2018). The community composition of copepods also changed from mostly large calanoid copepods to small cyclopoid copepods, and this was attributed to changes in prey size selection by sardines and anchovy (Verheye *et al.* 1998).

Marine mammals (including baleen whales), seabirds and fish are all part of higher trophic feeders that rely on plankton productivity, which forms the base of food webs in large marine ecosystems, including the SBUS (Verheye *et al.* 2016). The distribution of feeding baleen whales is a useful indication of where there is oceanographic productivity (Moore *et al.* 2002; Friedlaender *et al.* 2006). One example of such indication is the presence of large aggregations (20 – 200 individuals) of humpback whales (*Megaptera novaeangliae*, HBWs) in the SBUS between St Helena Bay and Cape Point from October to November (Findlay *et al.* 2017). These HBW "super-groups" are marked with densely packed individuals, displaying feeding behaviours such as lunging, diving, and defecating (Findlay *et al.* 2017). The environmental conditions that lead to these aggregations includes increased primary production and retention within the SBUS (Dey *et al.* 2021). Therefore, it is not surprising that right whales feed in the SBUS (Barendse and Best 2014), which clearly presents sufficient food resources for baleen whales. However, the extent to which right whales use the west coast as a feeding ground remains unknown.

1.3 STUDY RATIONALE, AIMS AND OBJECTIVES

The BCLME on the southwestern region of Africa, is one of four major EBUSs in the world. In these systems, equatorward winds blow along continents and move warm surface water offshore, which is then replaced with cold, nutrient-rich water from depth (Wang *et al.* 2015). The nutrients transported to the surface enhances the primary productivity in these upwelling areas; in fact, while EBUSs only cover around 2% of the ocean surface, they are responsible for 7% of the primary production in marine ecosystems globally (Pauly and Christensen 1995). Marine mammals, seabirds and fish are all part of higher trophic feeders that rely on plankton productivity, which forms the base of food webs in large marine ecosystems (Verheye *et al.* 2016). While the BCLME supports a high diversity of marine species, including baleen whales (Findlay *et al.* 2017, Kirkman *et al.* 2019), it also experiences high levels of anthropogenic activities, such as artisanal/commercial fishing, extensive shipping and coastal developments, leading to habitat transformation and pollution (Heileman and O'Toole 2008). Additionally, due to its high productivity and location inside South Africa's EEZ, the SBUS (a subsystem of the BCLME), is one of the focus areas of "Operation Phakisa", an initiative designed to unlock the Economic Potential of South Africa's Oceans. Therefore, there is an increasing potential for conflict between ocean economy sectors and the environment and great motivation to gather contemporary data on right whale feeding ecology which can be used in conservation and mitigation management of the population under "Operation Phakisa."

Aside from large aggregations of HBWs feeding in the SBUS (Findlay *et al.* 2017), right whales are also known to forage in the region (Barendse and Best 2014). However, the feeding ecology of the species in the SBUS remains unstudied.

Therefore, this study aims to provide an initial understanding of the feeding ecology of right whales on the South African west coast through these objectives: (1) Assess the component of the population feeding on the west coast; (2) evaluate targeted prey; and (3) describe feeding behaviour.

CHAPTER 2 SOUTHERN RIGHT WHALE FEEDING ECOLOGY ON THE SOUTH AFRICAN WEST COAST

2.1 ABSTRACT

South African southern right whales (*Eubalaena australis*, right whales) migrate between coastal calving, and offshore feeding grounds every year. However, this population also has a coastal, low latitude feeding ground on the South African west coast, which is situated in the vigorously productive Southern Benguela Upwelling System (SBUS). To better understand the extent to which the population uses the west coast as a feeding ground, the current study aimed to 1) assess the component of the population engaged in west coast feeding 2) evaluate targeted prey species 3) describe feeding behaviour. Results showed that mostly female right whales use the west coast as a feeding ground, especially those with an associated calf, suggesting that the west coast may be an opportunity for these females to build up energy reserves prior to migration. Results also showed that right whales target large copepods of the Genus *Calanoides*, which are upwelling specialists, and dominate within the SBUS. In more recent years, right whales did not feed at the surface, but anticipated dives and fed at depth during observational periods as opposed to more frequent surface feeding behaviour observed in 2004 – 2009. This may suggest a possible change in the distribution of dense prey patches to deeper layers within the water column. Overall, data presented here indicates that the west coast of South Africa may be an important feeding ground for South African right whales, all of which target mainly copepods.

2.2 INTRODUCTION

Southern right whales (*Eubalaena australis*, right whales) earned their common name from English whalers, who believed that they are the ideal ("right") whale to hunt, since they swim slowly near the shore, float when dead and yield significant amounts of oil and baleen (Allen 1916; Best 2007). Widespread exploitation around the globe brought the global population of right whales close to extinction (Dawbin 1986; Du Pasquier 1986). As a result, a ban of right whale commercial whaling was implemented in 1935 by the International Convention for the Regulation of Whaling (IWC 2001). Which has led to strong recovery of right whale populations in their main calving grounds, including Argentina/Brazil, Australia/New-Zealand and South Africa (Cooke *et al.* 2001; Groch *et al.* 2005; Bannister 2009; Carroll *et al.* 2013; Brandão *et al.* 2018).

It is believed that both female and male right whales have high fidelity to winter calving grounds (IWC 2001; Rowntree *et al.* 2001; Carroll *et al.* 2013) and summer feeding grounds (Best 2000; Valenzuela *et al.* 2009; Carroll *et al.* 2020), between which they migrate every year (Cummings 1985). The South African south coast is the primary calving ground for the South African population of right whales (IWC 2013), and this population likely has important offshore feeding grounds at the Subtropical Convergence, and the Polar Front (Mate *et al.* 2011). However, various sources of data also show they also use the South African west coast as a feeding ground (Best 2006; IWC 2013; Barendse and Best 2014).

The Benguela Current Large Marine Ecosystem (BCLME) on the South African west coast is an Eastern Boundary Upwelling System where alongshore winds force surface waters offshore which is then replaced with cold, nutrient-rich water from depth (termed Ekman transport) (Wooster and Reid 1963; Sverdrup 1983; Wang *et al.* 2015). This upwelling of deeper waters to the euphotic zone (light zone) brings nutrients to phytoplankton that use it during photosynthesis, resulting in phytoplankton blooms. As a result, the BCLME is one of the most vigorously productive marine ecosystems in the world (Cushing 1969; Ryther 1969). The BCLME is separated into two subsystems, the northern Benguela and Southern Benguela Upwelling System (SBUS) (Hutchings *et al.* 2009). It is important to understand that upwelling in the SBUS is strongly seasonal (Verheye *et al.* 2016; Lamont *et al.* 2018), and that upwelling-favourable winds peak in summer and autumn (Hutchings *et al.* 2009). In addition, upwelling-favourable winds lead to high primary productivity in discrete upwelling areas, for example off Cape Columbine, during summer (Huggett *et al.* 2009; Jarre *et al.* 2015). Zooplankton, like copepods and krill, then feed on the phytoplankton (primary consumers) (Kiørboe 1993; Lenz 2000), making zooplankton abundance particularly high north of Cape Columbine, especially in the retentive environment of St Helena Bay (Verheye *et al.* 1992). Right whales feed primarily on large quantities of zooplankton, including copepods, krill, pteropods or larval stages of other crustaceans (Cummings 1985; Reilly *et al.* 2004; Baumgartner *et al.* 2007). Consequently, the area is favourable for baleen whales, like humpback whales (*Megaptera novaeangliae*, HBWs) and right whales, to feed during summer months (IWC 2013; Barendse and Best 2014; Findlay *et al.* 2017).

The zooplankton abundance in the SBUS can vary temporally; for example it increased significantly between 1951 – 1996 (Verheye *et al.* 1998). This was likely due to a decrease in predation pressure from sardines and anchovy, and an intensification of upwelling in the region (Verheye *et al.* 1998). The community composition of copepods also changed from mostly large calanoid copepods to small cyclopoid copepods, and this was attributed to changes in prey size selection by sardines and anchovy (Verheye *et al.* 1998). In general, the calanoid copepod, *Calanoides carinatus*, dominates in the SBUS (Verheye 1991) because its abundance increases rapidly during upwelling events, therefore making it an “upwelling specialist” (Borchers and Hutchings 1986; Peterson and Painting 1990). Considering its high abundance, it is hypothesized this species forms the main diet of right whales feeding in the South African west coast.

As filter feeders, right whales need dense prey patches to filter effectively, and they will manoeuvre through the water based on changes in prey density (Kenney *et al.* 1986; Baumgartner and Mate 2003; Michaud and Taggart 2007). On the one hand, the speed of manoeuvring can be rapid, as seen in South Georgia where right whales were feeding on highly mobile krill (Calderan *et al.* 2023). On the other, right whales captured copepods by swimming slowly and methodically (Kraus *et al.* 2007). Therefore, the speed of manoeuvring seems to change depending on the size and mobility of the prey that needs to be captured (Calderan *et al.* 2023). Also, krill and copepods migrate between deeper and shallower layers to avoid predation by visual predators (Bollens and Frost 1989; Hays 1995; Falk-Petersen *et al.* 2008; Baumgartner *et al.* 2011). For example, krill migrate to shallower depths at dusk to feed, thereby decreasing predation risk by feeding in reduced light (Klevjer *et al.* 2010). In contrast, large copepods migrate to deeper, darker depths during the day as the risk of predation outweighs the reward of feeding in shallower depths where they can be easily spotted (Huntley and Brooks 1982; Bollens and Frost 1989; Hays 1995; Falk-Petersen *et al.* 2008; Baumgartner *et al.* 2011). The result is that prey density is not uniform throughout the water column, and more importantly, prey density changes on a temporal scale (Goldbogen *et al.* 2017b).

In the SBUS, right whales have been observed feeding at the surface, just below the surface as well as at depth (Barendse and Best 2014). However, so far, no assessment has been done on which prey these whales target and how their feeding behaviour may be related to this. Since right whales feed mainly on copepods north of 40°S (Tormosov *et al.* 1998), and copepods are known to be the most abundant zooplankton species in the SBUS, it is expected that right whales will predominantly target copepods and therefore would display slow, methodical feeding (Kraus *et al.* 2007), instead of high-speed movements like right whales feeding on krill (Hamner *et al.* 1988; Calderan *et al.* 2023). Also, since not much is known about the distribution and seasonal occurrence of right whales on the west coast (Barendse and Best 2014), this study aims to assess the age class and sex of the right whales using the west coast as a feeding ground.

2.3 MATERIALS AND METHODS

2.3.1 STUDY SITE

Data were collected during boat-based and aerial surveys along the South African west coast between St Helena Bay (32°44' S, 18°0' E) a semi-enclosed bay, with water depth approximately 130m, situated north of Cape Columbine, and Cape Point (34°21' S, 18°29' E) located approximately 110km south from Cape Town (Figure 1).

2.3.2 DATA COLLECTION

Photo-identification

Aerial surveys were conducted between Cape Point and St Helena Bay, in autumn, spring, and summer of 2022 by using a lightweight autogyro. This small-type aircraft uses an unpowered rotor in autorotation to generate lift, and an engine-powered propeller, like that of a fixed-wing aircraft, to provide thrust. It is a fuel-efficient aircraft that allows for cost-effective monitoring of an extended coastal strip compared to an aeroplane or helicopter. Two passengers can fit into an autogyro; the pilot who sits in the front and an observer in the rear. Due to the engine-powered propeller and an unpowered rotor, the autogyro has no hovering capabilities and is often an open configuration.

The aerial surveys were flown at an altitude of approximately 300m, at a speed of approximately 60kts and at a distance of 500m offshore. During the surveys, the pilot mainly searched ahead and coastwise, while the observer in the rear searched offshore. Intercom communication between the pilot and the observer allowed the observer to make notes of the right whales counted both inshore and offshore. If whales were too far offshore to determine group composition, they were approached, after which the aircraft returned to a distance of approximately 500m offshore. If the presence of a calf could not be determined with certainty, the observed whale was recorded as unaccompanied, and the survey continued. All right whales observed during the survey were counted and photographed for photo-identification purposes.

Additionally, whales previously identified on the South African west coast (either opportunistically or from dedicated aerial surveys; see Best 1990) were extracted from the South African national photo-identification catalogue and sighting history database (from MRI Whale Unit) spanning the period 1979 – 2022, which includes 2 103 known individuals and their sighting location.

Boat-based surveys

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Boat-based surveys were conducted in November 2022 and January 2023 in good weather conditions (i.e., sea state ≤ Bf 3). These surveys were conducted from a 6m semi-rigid inflatable boat with a spotter chair positioned 3m above sea level. The boat was launched from harbours in St Helena Bay (32°44' S, 18°0' E), Langebaan (33°2' S, 18°2' E), and Yzerfontein (33°20' S, 18°8' E). Once a whale was spotted, the coordinates, sea surface temperature, sea state, date and time and whale behaviour (see further for details) were recorded. Group composition was also recorded, indicating if a whale was unaccompanied, with an associated calf, or in a group with other whales.

Data were also available from boat-based surveys conducted in St Helena Bay in the period 2003 – 2009. These data also contained the coordinates of spotted whales, as well as the surface temperature, sea state, date and time and group composition and whale behaviour.

Prey and faecal sampling

Targeted and available prey was sampled by means of prey hauls using a 300micron net. To assess available prey, prey hauls were performed in a control line of stations located in St Helena Bay approximately 5nm apart (defined as "station prey hauls") (see Figure 1). Location of these stations were originally chosen in 2003 by the MRI Whale Unit as it was within the larger area where right whales were seen feeding for the first time (samples available from 2003 – 2007; MRI Whale Unit, unpublished data). To allow for direct comparison, the same stations were sampled in this study.

In the current study, as well as for the samples collected between 2003 – 2007, prey hauls were also performed near right whales that were believed to be feeding (defined as "target prey hauls") (see Figure 1); i.e., if the whale was presumed feeding at depth, or exhibiting specific feeding behaviours at the surface (baleen flushing, head nodding, etc; see Table 1). If the whale appeared to be feeding at depth, the net was dropped and lifted vertically through the water (termed "vertical prey haul'). Contrastingly, if the whale was seen feeding at the surface, the net was dragged horizontally through the water (termed "horizontal prey haul"). All target hauls occurred at a minimum distance of 50m from the feeding whale, so as not to disturb the animal and to prevent entanglement. All plankton samples were placed into 250ml plastic flasks and fixed with 70% ethanol on the boat and left for 24hrs for the plankton to settle. After this period, the samples were topped-up with fresh ethanol and stored until the samples were processed.

As whale faeces float at the surface after defecation (Rolland *et al.* 2006), faecal samples were taken, when possible, using a 250micron net. The faecal samples were then placed into 250ml flasks in the boat and kept frozen until processing.

Behavioural observations

For behavioural observations in November 2022 and January 2023, the boat approached a focal right whale slowly (approximately 5-10km/h) in a parallel manner, up to a minimum distance of 100m to minimise disturbing the natural behaviour of the whale. The behavioural data of the focal whale was gathered using a focal 5-min point sampling method; every 5 minutes, the behaviour of the whale was recorded using the following categories: travelling, resting, feeding, underwater, other (see Table 1 for definitions of these behaviours). Minimum duration of a behavioural observation period was 20min (4 x 5-min samples).

Table 1. Behavioural categories, and their descriptions, assigned to right whales observed during boat-based surveys.

Behavioural category	**Description or associated behaviour**
Travelling	Moving steadily between locations while leaving surface “flukeprints” (Lusseau 2003).
Resting	Lying motionless at the surface (Lusseau 2003).
Feeding	• Mouth open while skimming the surface. • Baleen flushing: removing prey from baleen by rapid closure of mouth and simultaneous expulsion of water at the surface (Mayo and Marx 1990). • Head nodding: vigorous shaking of the head from side-to-side above the surface to mechanically shake prey items off baleen (Werth 2001).
Underwater	• Whale is below the surface. • Diving: the entire fluke of the whale is visible above the surface, and the downward trajectory of the whale is perpendicular to the surface.

Other	Behaviour not clearly fitting into the above categories.

Behavioural data were also available from the MRI Whale Unit (unpublished data) that were collected in the period 2004 – 2009 in St Helena Bay. During this period, behaviour was sampled using the same behavioural categories as mentioned above (Table 1). However, behaviour was noted continually during the observational period i.e., behaviour was noted as it occurred and not on a 5-min bases as in the current study. Consequently, 5-min point samples were extracted from the 2004 – 2009 data for data comparison between the two collection periods.

2.3.3 DATA ANAYLSIS

Photo-identification

Right whales have patches of keratinized skin, called callosities, which house ectocommensal crustaceans (cyamids or whale lice). Every whale has a unique callosity pattern; making it useful to identify individuals in photo-identification (Payne *et al.* 1983). The photo-identification photographs obtained from the aerial surveys were matched to the South African national catalogue (containing 2 103 individuals) using the Hiby-Lovell automated computer-based image recognition and associated database system, which utilizes digitized extracts of the callosity patterns (automatically adjusted for tilt and inclination) to make inter-individual comparisons. Automated comparisons of callosity patterns were rated for similarity using digital algorithm indices of similarity from 1.00 to zero, and the most similar candidate was presented first. Matching by eye started with the highest index and continued until a match was made or until the index had fallen to 0.50, although the performance of the system is such that the actual match can be found in the first 3 candidates in over 90% of the cases. A matched sighting was then recorded in a catalogue. If no match was found, the individual was assigned a unique identification number and incorporated into the catalogue as a new individual.

Adding all available photo-identification data from the national right whale catalogue, assessments were made on the sex, age class and previous sighting history of the whales seen on the South African west coast.

Inferences on age class were made based on proportion of head to body length (with adults having a head at 1/3rd of the total body length). Right whales were classified as females when they were observed in close association with a calf.

Prey samples

All zooplankton samples were decanted into measuring cylinders and allowed to settle for 24hrs. The settled volume, as well as the sample volume, was recorded for each sample. The sample was then suspended in a known volume (suspension volume), and mixed until the zooplankton were evenly distributed. Three 2ml subsamples were then collected using a pipette, and each subsample was pipetted into a Bogorov counting tray and examined under a stereo microscope (Nikon SMZ1500). Individuals within zooplankton groups of interest were counted, and the total abundance of each zooplankton group per sample was calculated by dividing the suspension volume by two and multiplying it with the average count across the three subsamples. To estimate the volume filtered by the net (filtered volume), the area of the net mouth was multiplied by the net depth (measured by a flowmeter). The density (m^{-3}) of zooplankton groups per sample was then calculated by dividing the zooplankton abundance by the filtered volume. A Wilcoxon rank-sum test was used to test significant differences in the average density of zooplankton groups between station and target hauls.

Faecal samples

Following D’Agostino *et al.* (2016), each faecal sample was homogenized and three subsamples (3ml) were taken from the samples. Then, each subsample was washed onto a 67µm Nylon mesh filter. The retentate was mixed with 15ml distilled water, and 1.5ml sodium hypochlorite (5.5% active chlorine) was added. The solution was then left for 1hr 30min, after which it was washed with distilled water onto a 67µm Nylon mesh filter. The retentate was then mixed with 10ml distilled water, and 2ml methylene blue was added to the solution for the staining of zooplankton remains.

The zooplankton remains in the subsamples were examined under a stereo microscope (Nikon SMZ1500). All remains were assigned to three zooplankton groups and counted: bivalves, copepods and euphausiids, (which were assumed to be the main zooplankton groups detectable in faecal material as they are made of chitin, and are indigestible (Stone *et al.* 1988; Menéndez *et al.* 2007)). Data were pooled from all three subsamples for a final count per faecal sample. The proportion of bivalves, copepods and euphausiid remains found within the faecal samples were then compared to the proportion of these zooplankton groups within the target haul samples.

Behavioural analysis

Behavioural data were first analysed in terms of behavioural proportions in order to determine which behaviours were most commonly observed among whales on the west coast. These data were also analysed separately as time-discrete Markov chains, where the transition probability from one observed behaviour to the next was determined by:

$$Transition\ probablity\ (p) = \frac{a}{i}$$

- *a* = number of times a given behaviour (*i*) transitioned to any succeeding behaviour (*j*)
- *i* = total number of times a given behaviour (*i*) was seen as the preceding behaviour

A Welch Two Sample t-test was conducted to test for a difference in the mean transition probabilities from underwater to a succeeding behaviour between November 2022 and January 2023 to determine whether there was a greater chance of whales remaining underwater in January compared to November. All statistical analyses were performed using R 4.3.1 (R Core Team, 2023).

2.4 RESULTS

Boat-based surveys resulted in a total effort equated to 97hrs 8min (42hrs 39min in November and 54hrs 29min in January), with a total travel distance of 1 350.8km. The boat was launched from three different harbours including St Helena Bay, Yzerfontein and Langebaan. Despite effort in all three areas, whales were only encountered in Yzerfontein (Figure 1).

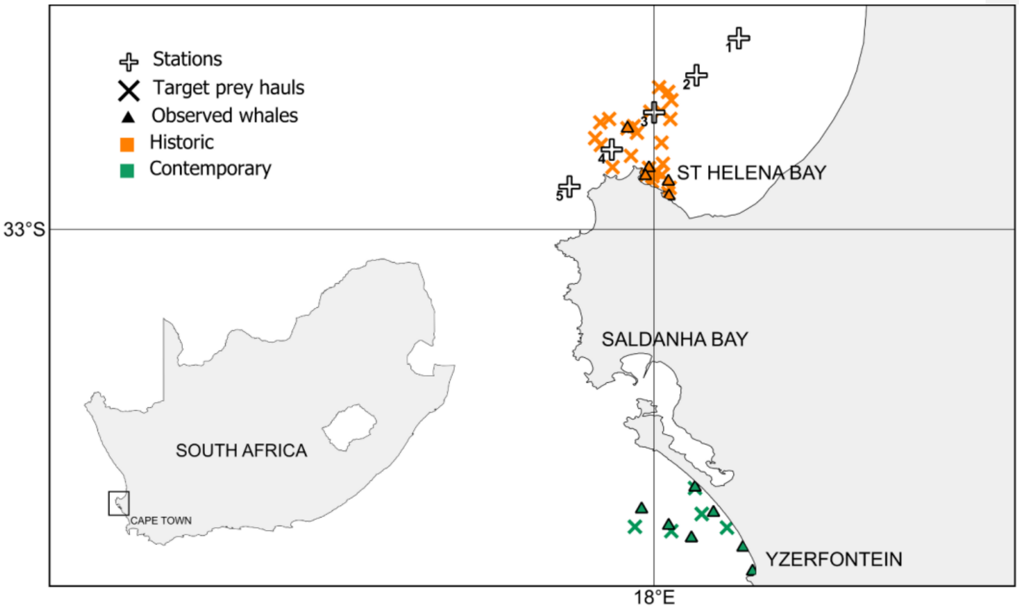

Figure 1. The study area indicating prey haul stations (plus symbols) and target prey hauls (crosses) done near presumed feeding right whales off the South African west coast. Whale behaviour was also observed during observational follows (triangles). The difference in symbol colour distinguishes between data collected in previous years by the MRI Whale Unit, between 2003 – 2009 (orange) and during this study (2022 – 2023, green). The study area is indicated by a square on the insert of South Africa.

2.4.1 PHOTO-IDENTIFICATION

A total of 75 right whales were photographed on the South African west coast for individual identification between 1979 – 2022. Of these, 70 whales were classified as adults and 5 as juveniles. Sex of the individual could only be determined for 50 individuals, all classified as female (49 adult females due to close association with a calf, and 1 juvenile, based on its partial grey dorsal colouration (Schaeff *et al.* 1999). This juvenile was first seen as a calf in 2019 on the south coast calving ground, and classed as a juvenile when photographed on the west coast 3 years later, in 2021. The sex of the remaining 25 individuals could not be determined (Figure 2).

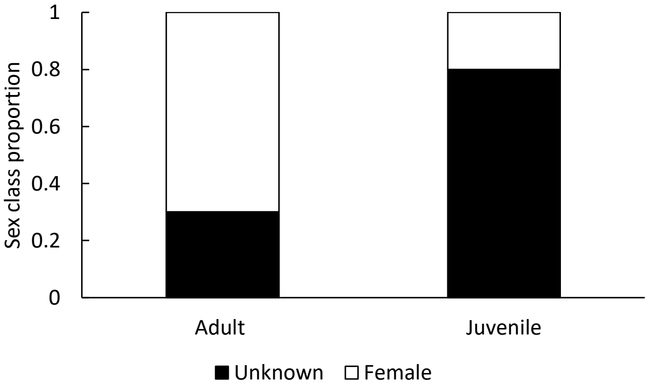

Figure 2. The proportion of adult and juvenile right whale individuals photographed for photo-identification purposes on the South African west coast (between 1979 – 2022)

When comparing photo-identification images to the existing national identification catalogue of the South African right whale population, matches could be found for 35 of the confirmed adult females (N = 49). The majority of the matches (74%) related to females that were sighted during annual aerial surveys on the south coast between 1 and 4 years, whereas lower proportions related to matches for females sighted over more years (Table 2). Of the confirmed adult females (N = 49), 13 were not matched to individuals within the catalogue, but were identified and confirmed as adult females due to their association with a calf when they were first photographed on the west coast.

Table 2. The number of years female adult right whales identified on the South African west coast (N = 49) have been sighted on the south coast during annual aerial surveys between 1979 – 2022.

Number of years females sighted during south coast aerial surveys	Proportion (%)
1	8.2
2	16.3
3	20.4
4	8.2
5	4.1
6	10.2
7	2.0
8	0.0
9	0.0
10	2.0

Throughout the aerial surveys between 1979 – 2022, 47 cow/calf pairs were present on the west coast, and 13 of these cow/calf pairs have only exclusively been seen on the west coast. In addition to these cow/calf pairs, two more were encountered in November 2022 during the boat-based surveys in the current study.

2.4.2 PREY

Prey hauls

A total of 17 prey hauls were performed during fieldwork in November 2022 and January 2023, of which 7 were targeted prey hauls and 10 were station prey hauls, with two hauls performed at each station (Figure 1). The results of this section are summarized in the table at the end of this section (Table 3).

Results showed that small copepods of the Genus *Clausocalanus, Ctenocalanus, Paracalanus,* and *Calocalanus* as well as copepods in the Family Calanidae amounted to 20.8% of the total abundance in all 17 prey hauls. Smaller abundances were found in the other copepod groups, with Family Centropagidae (cen; 8.2%), Family Metridinidae (met; 3.9%), Family Eucalanidae (euc; 0.8%), and Family Candaciidae (can; 0.3%). Among the non-copepod groups, bivalves were the least abundant, amounting to only 0.3% of the total abundance in 17 prey hauls. Family Euphausiidae made up only 4.8% of the total abundance, and zooplankton groups that were not copepods, bivalves or euphausiids combined (other) amounted to 40.2%.

In the target hauls alone, Family Calanidae (665.9 m^{-3} ± 1 478.6) had the greatest average density of all copepod groups followed by small copepods of the Genus *Clausocalanus, Ctenocalanus, Paracalanus, and*

Calocalanus (583.1 m^{-3} ± 1 089.5), Family Centropagidae (308.9 m^{-3} ± 747.9), Family Metridinidae (55.6 m^{-3} ± 55.3), Family Candaciidae (8.4 m^{-3} ± 22.3), and Family Eucalanidae (0.1 m^{-3} ± 0.2). Among the non-copepod groups, zooplankton classified as "other" had the greatest average density (629.1 m^{-3} ± 623.2), followed by Family Euphausiidae (344.2 m^{-3} ± 534.2) and bivalves (25.3 m^{-3} ± 66.8) (Figure 3).

In station hauls, zooplankton groups classified as "other" had the greatest average density (747.6 m^{-3} ± 850.7). This group was followed by all 6 copepod groups, from highest to lowest average density: small copepods of the Genus *Clausocalanus, Ctenocalanus, Paracalanus, and Calocalanus* (295.7 m^{-3} ± 174.2); Family Calanidae (292.1 m^{-3} ± 288.4); Family Centropagidae (145.8 m^{-3} ± 204.9); Family Metridinidae (48.0 m^{-3} ± 33.7); Family Eucalanidae (13.7 m^{-3} ± 14.8); and Family Candaciidae (4.0 m^{-3} ± 12.6). The two lowest average densities in station hauls were recorded for bivalves (2.1 m^{-3} ± 6.7) and Family Euphausiidae (1.2 m^{-3} ± 3.0) (Figure 3).

Comparing the station and the target hauls, it was revealed that copepods of the Family Eucalanidae was significantly more densely present in the station hauls than the target hauls (Wilcoxon rank-sum test: $W = 58$; $p = 0.01$). No significant difference in the median density of any other zooplankton groups between station and target hauls were found (Figure 3).

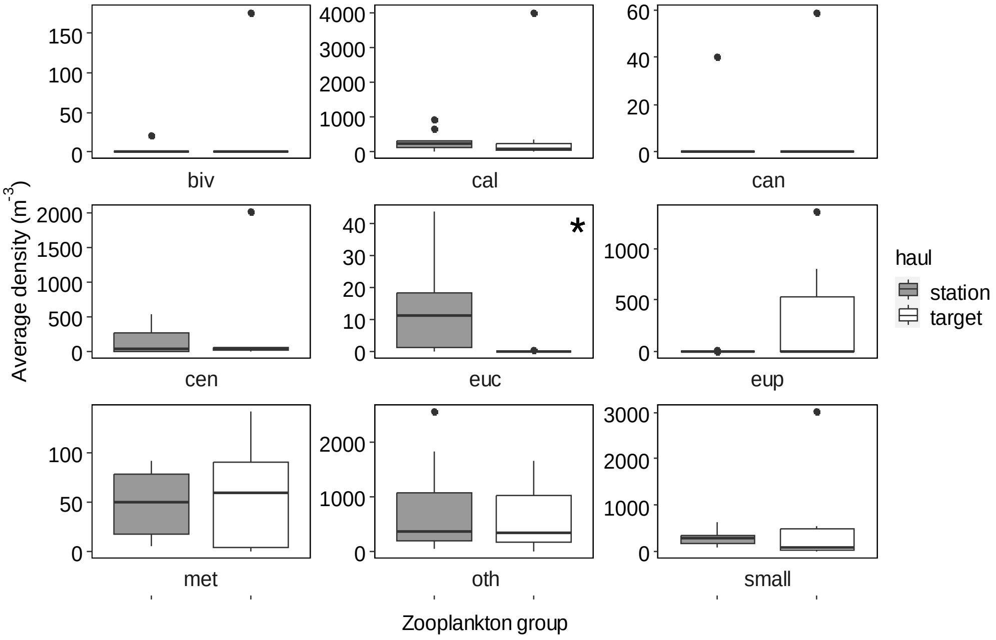

Figure 3. Average density (m^{-3}) of zooplankton groups in prey hauls performed at 5 stations situated within St Helena Bay (station); as well as near presumed feeding right whales (target) in 2022 – 2023. Zooplankton groups other than copepods, bivalves (biv) or Family Euphausiidae (eup) were classified as other (oth). Small copepods (small) are those of the Genus *Clausocalanus*, *Ctenocalanus*, *Paracalanus*, and *Calocalanus*. Other copepods were grouped according to Family: Calanidae (cal); Candaciidae (can); Centropagidae (cen); Eucalanidae (euc); Metridinidae (met). Significant difference in medians between station and target hauls is indicated by an asterisk.

A total of 203 prey hauls were done in 2003 – 2007 by the MRI Whale Unit (unpublished data) (target: N = 38; station: N = 165, Figure 4). Some stations had more prey hauls than others: station 1: n = 36; station 2: n = 42; station 3: n = 43; station 4: n = 30; station 5: n = 23. Of all prey hauls, the Family Calanidae were the most abundant zooplankton group (23.8%), followed by small copepods of the Genus *Clausocalanus, Ctenocalanus, Paracalanus, and Calocalanus* (23.1%), bivalves (20.3%), zooplankton groups other than copepods, euphausiids or bivalves (oth; 13.1%), Family Metridinidae (10.3%), Family Centropagidae (8.9%), Family Eucalanidae (0.2%), Family Euphausiidae (0.01%), and Family Candaciidae (0.003%).

Results showed differences in the average density of zooplankton groups in both target and station hauls. In target hauls, the highest average density recorded was for the Family Centropagidae (11 209.7 m^{-3} ± 57 407.4), followed by Family Calanidae (8 483.5 m^{-3} ± 12 276.2), small copepods of the Genus *Clausocalanus*, *Ctenocalanus, Paracalanus*, and *Calocalanus* (8 386.9 m^{-3} ± 14 496.5), and Family Metridinidae (2 359.5 m^{-3} ± 5 498.0). Of the non-copepod groups, other zooplankton had the highest density (other: 1 918.5 m^{-3} ± 6 049.7), followed by bivalves (1 804.3 m^{-3} ± 3 800.0). The Family Euphausiidae were not present in the target hauls. The lowest density found in target hauls was for Family Eucalanidae (27.4 m^{-3} ± 66.0) and Family Candaciidae (5.2 m^{-3} ± 32.2) (Figure 4).

In station hauls, zooplankton of the Family Calanidae had the highest average density (3 010.2 m^{-3} ± 5 552.3), followed by small copepods of *Clausocalanus*, *Ctenocalanus, Paracalanus*, and *Calocalanus* (2 843.4 m^{-3} ± 3 871.3), bivalves (2 461.6 m^{-3} ± 7 600.7) and zooplankton groups classed as “other” (1 844.3 m^{-3} ± 3 387.2). Family Metridinidae (1 277.7 m^{-3} ± 2 314.4), Family Centropagidae (759.3 m^{-3} ± 2 510.3), Family Eucalanidae (26.6 m^{-3} ± 61.5) and Family Candaciidae (0.1 m^{-3} ± 1.6) had the 4 lowest average densities in station hauls. Of the non-copepod groups, Family Euphausiidae had the lowest average density in station hauls (2.2 m^{-3} ± 16.0) (Figure 4).

Comparing station and target hauls collected between 2003 – 2007, a slight difference could be found between the median average density in Family Calanidae, small copepods of *Clausocalanus*, *Ctenocalanus, Paracalanus*, and *Calocalanus*, and other zooplankton groups classed as “other”. However, a Wilcoxon rank-sum test revealed that this difference was only significant for the Family Calanidae (W = 2481; target: N = 38; station: N = 165; p = 0.04) and in zooplankton group classed as “other” (W = 3815; target: N = 38; station: N = 165; p = 0.03) (Figure 4).

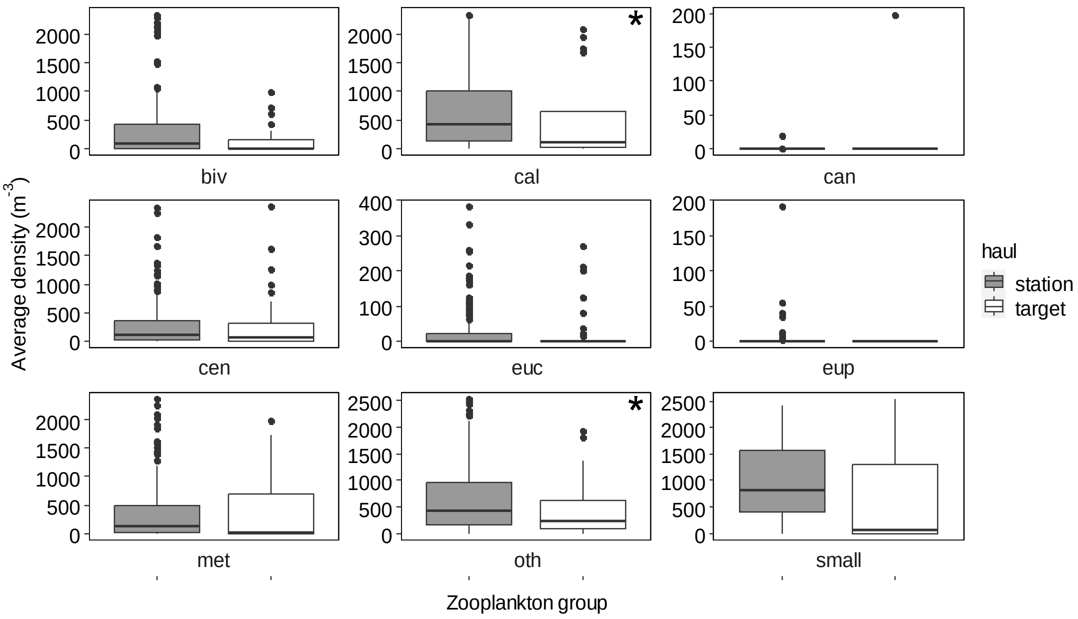

Figure 4. Average density (m^{-3}) of zooplankton groups in prey hauls performed at 5 stations situated within St Helena Bay (station); as well as near presumed feeding whales (target) in the period 2003 – 2007. Zooplankton taxa other than copepods, bivalves (biv) or Family Euphausiidae (eup) were classified as "other" (oth). Small copepods (small) are those of the Genus *Clausocalanus, Ctenocalanus, Paracalanus,* and *Calocalanus.* Other copepods were grouped according to Family: Calanidae (cal); Candaciidae (can); Centropagidae (cen); Eucalanidae (euc); Metridinidae (met). Significant differences between density in station and target hauls are indicated by an asterisk.

Comparing zooplankton abundance between all contemporary (2022 – 2023) and historic (2003 – 2007) prey hauls, small copepods (*Clausocalanus, Ctenocalanus, Paracalanus,* and *Calocalanus*) and zooplankton of the Family Calanidae made up around 20% of the total zooplankton abundanc in both collection periods. There are other similarities as well, like the low abundance of Family Centropagidae (around 8 – 9%) and families Eucalanidae and Candaciidae (< 1%) (Table 3). Also, when comparing the abundance of genera within Family Calanidae, results showed that *Calanoides* was the most abundant in both contemporary (60.9%) and historic prey hauls (98.2%). Genus *Calanus* made up 26.2% within the Family in contemporary hauls, and 1.8% in historic hauls. Genus *Nannocalanus* was the least abundant with 12.9% in contemporary hauls, and 0.3% in historic hauls. Noticeable differences were seen in “other” zooplankton groups, that accounted for 40.2% in contemporary abundance, but only 13.1% in historic abundance; in addition, bivalves had a negligible abundance (0.3%) in contemporary hauls, but 20.3% in historic hauls (Table 3).

For station hauls, results suggest that little has changed between historic and contemporary collection periods. Small copepods and copepods within the Family Calanidae were the two most densely available copepod prey in both historic and contemporary station hauls, followed by Families Centropagidae, Metridinidae, and very low densities of Families Eucalanidae and Candaciidae (Table 3).

The density of zooplankton near presumed feeding whales (target hauls) were similar in that Family Calanidae and small copepods had high densities both historically and contemporarily. Furthermore, bivalves, and Families Eucalanidae and Candaciidae were the three least dense groups historically and contemporarily. However, Family Centropagidae had the highest density historically (Table 3).

Table 3. The average proportion (%) of zooplankton groups in all prey hauls, including the average proportion (%) of *Genus Calanus*, *Calanoides* and *Nannocalanus* within Family Calanidae. Also shown is the average density (m^{-3}) of zooplankton groups within station and target hauls done near presumed feeding whales during two collection periods (2022 – 2023 and 2003 – 2007).

Proportion (%)			Density (mean ± SD)			
			Prey haul type			
			Station	Target	Station	Target
Zooplankton group	2022 – 2023	2003 – 2007	2022 – 2023		2003 – 2007	
Bivalves	0.3	20.3	2.1 ± 6.7	25.3 ± 66.8	2 461.6 ± 7 600.7	1 804.3 ± 3 800.0
Family Calanidae	20.8	23.8	292.1 ± 288.4	665.9 ± 1 478.6	3 010.2 ± 5 552.3	8 483.6 ± 12 276.2
Genus Calanus	26.2	1.8	-	-	-	-
Genus Calanoides	60.9	98.2	-	-	-	-
Genus Nannocalanus	12.9	0.3	-	-	-	-
Family Candaciidae	0.3	0.003	4.0 ± 12.6	8.4 ± 22.3	0.1 ± 1.6	5.2 ± 32.2
Family Centropagidae	8.2	8.9	145.8 ± 204.9	308.9 ± 747.9	759.3 ± 2 510.3	11 209.7 ± 57 407.4
Family Eucalanidae	0.8	0.2	13.7 ± 14.8	0.1 ± 0.2	26.6 ± 61.5	27.4 ± 66.0
Family Euphausiidae	4.8	0.01	1.3 ± 3.0	344.2 ± 534.2	2.2 ± 16.0	0 ± 0
Family Metridinidae	3.9	10.3	48.0 ± 33.7	55.6 ± 55.3	1 277.7 ± 2 314.4	2 359.5 ± 5 498.0
Other	40.2	13.1	747.6 ± 850.7	629.1 ± 623.2	1 844.3 ± 3 387.2	1 918.5 ± 6 049.7
Small copepods	20.8	23.1	295.7 ± 174.2	583.1 ± 1 089.5	2 843.4 ± 3 871.3	8 386.9 ± 14 496.5

Faecal sample analysis

Only 3 right whale faecal samples could be collected during fieldwork. In these samples, copepods made up the largest proportion of zooplankton remains (Sample 1 = 87%, Sample 2 = 89%, Sample 3 = 64%), more so than in the target hauls near presumed feeding whales (Figure 5). While euphausiids were present in the area where whales were feeding (and made up 5% of the target haul samples), no euphausiid remains were found in the whale faecal samples. Also, there seemed to be a greater proportion of bivalves found in the whale faecal samples (Sample 1 = 13%, Sample 2 = 11%, Sample 3 = 36%), compared to the proportion of bivalves present in the target haul samples (0.1%).

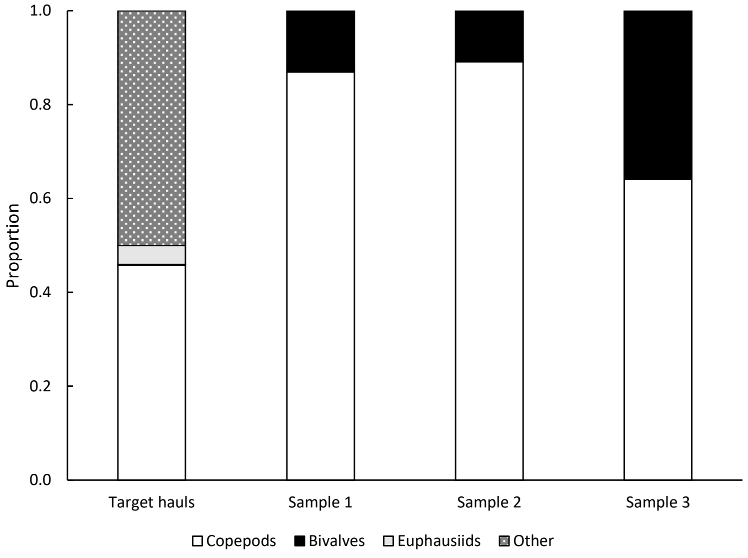

Figure 5. Proportions of copepods, bivalves and euphausiids in target haul samples done in January 2023 near presumed feeding right whales, as well as in faecal material sampled during the same field work season. “Other” includes zooplankton groups that were not copepods, bivalves and euphausiids (target hauls: N = 7; faecal samples: N = 3).

2.4.3 BEHAVIOUR

In total, there were 12 observational follows, of which 7 were contemporary (2022 – 2023) and 5 were historic (2004 – 2009). There was a longer total observation time contemporarily (5hrs 75min) compared to historically (3hrs 6min) and every observational period was between 10min – 1hr 30min (Table 4). Feeding-associated behaviours on the surface such as baleen flushing and head nodding was only seen in 2004 – 2009 and were included in the feeding category, while breaching, also only seen in 2004 – 2009, was classified as other.

Table 4. The total observation time (hrs) of behavioural focal follows done in the 2022 – 2023 (contemporary) and 2004 – 2009 (historic) collection periods.

	Contemporary (2022 - 2023)	Historic (2004 - 2009)
Focal follow nr	Observation time (min)	
1	90	90
2	25	40
3	85	15
4	60	25
5	30	50
6	20	-
7	35	-
Total observation time (hrs)	5hr 75min	3hr 6min

During observational periods, whales in November (which included 3 behavioural follows on one cow/calf pair, and 1 on a different cow/calf pair) seemed to move in lines near the coastline, compared to whales in January that had more localized movement further offshore, as illuded to by boat tracks during observational follows (Figure 6).

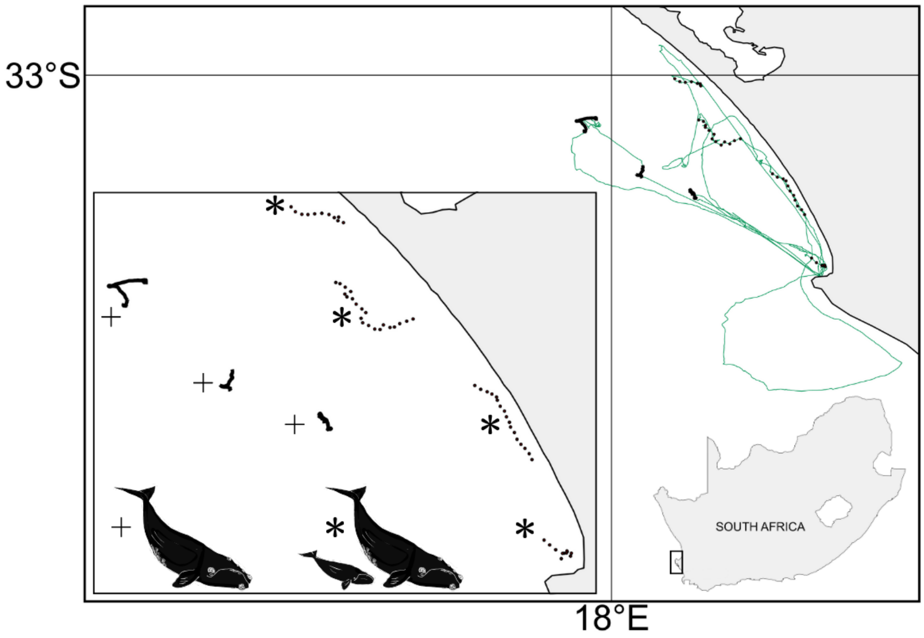

Figure 6. Boat effort tracks (green) while searching for right whales during the current study, with the insert providing a closer look at boat tracks during observational follows done in November 2022 (dotted) and January 2023 (solid). Whales observed in January were all unaccompanied (plus symbol), and group sizes ranged between 2 and 5 individuals. Observed cow/calf pairs are indicated by an asterisk. The study area is also indicated by a square on the map of South Africa.

Relative proportions of observed behaviours

In the contemporary observations (2022 – 2023), data showed that there was a significantly larger proportion of behavioural samples assigned to the category "underwater" than to any other category, indicating whales spent more time underwater than at the surface (resting = 21%; travelling = 13%; underwater = 67%; Chi-Square Goodness of Fit Test: X^2 (1, N = 100) = 9.00, p < 0.05).

Within each month, results indicated a significant difference within November 2022 (chi-Square Goodness of Fit Test: X^2 (2, N = 100) = 38.4, p < 0.0001) and January 2023 (chi-Square Goodness of Fit Test: X^2 (2, N = 100) = 69.2, p < 0.0001), with some encounters showing higher proportions of travelling and resting than others. However, at all times, the largest proportion of behavioural samples was assigned to underwater in both months (Figure 7).

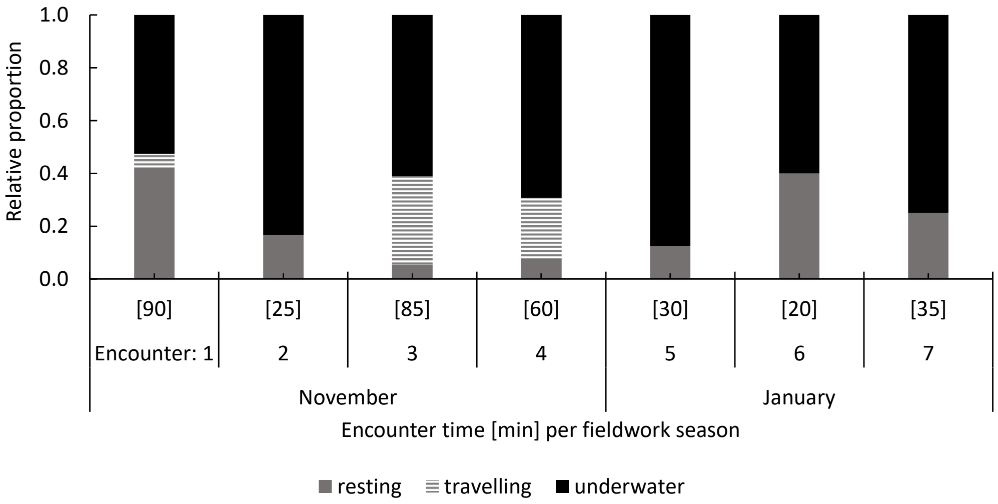

Figure 7. Variation in relative frequencies of behaviours in southern right whales on the South African west coast during summer months (N = 7).

When comparing the relative proportions of behavioural samples between months, no significant difference could be found, indicating whales had the same general behavioural pattern in November and January (Pearson's Chi-squared test: X^2 (3, N = 66) = 6.7, $p > 0.05$, Figure 8). However, some differences were apparent during field observations: firstly, right whales in November that were described as being underwater, did not seem to dive deep, but rather remained just below the surface before emerging again to travel, or to rest, with soft blows at the surface. However, whales in January described as being underwater dove to depth (showing tail flukes) and when they emerged, they had up to three consecutively hard blows while resting at the surface, indicative of hyperventilation and anticipation of dives (Hamner *et al.* 1988). Secondly, whales observed in November were frequently travelling slowly at the surface, while those observed in January were described in the field as “diving”, “presumed feeding”, “all flukes up when diving”, “blows”, “two individuals diving after each other”, “many blows from the entire group”, “blow, blow, dive”.

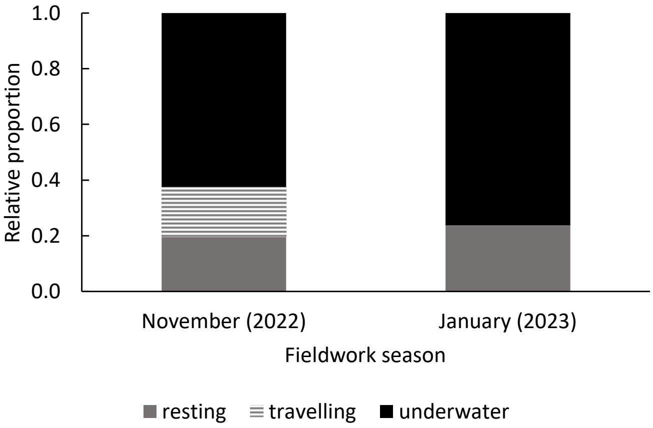

Figure 8. Relative proportions of behavioural samples from right whale individuals on the South African west coast during fieldwork conducted in November 2022, and January 2023 (2022: N = 56; 2023: N = 21).

When comparing between the historic (2004 – 2009) and contemporary (2022 – 2023) behavioural data, it appeared that feeding (as well as feeding-associated behaviours on the surface such as baleen flushing and head nodding) and “other” behaviours, had a higher relative frequency historically than contemporarily (Figure 9). Also, the behaviours of traveling and underwater were only observed in the contemporary years.

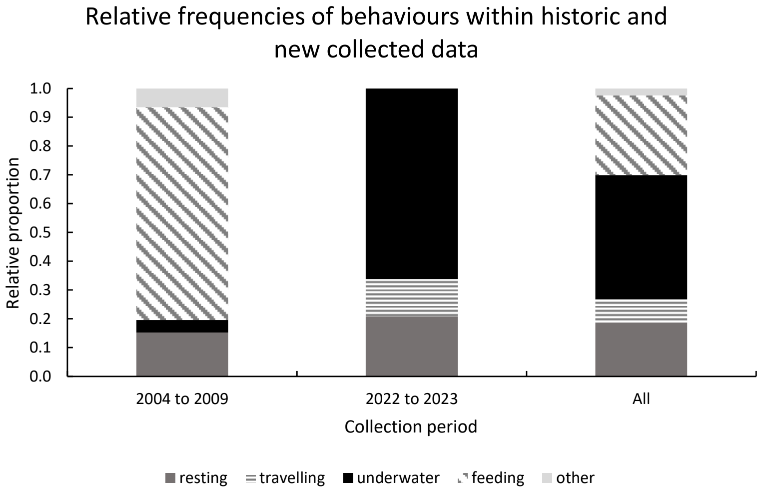

Figure 9. Variation in relative proportions of behavioural samples while observing in right whales on the South African west coast during historic (2004 – 2009) and contemporary (2022 – 2023) data collection periods.

Transition probability

In the 7 focal follows (November: N = 4, January: N = 3), whales that were underwater had a greater probability of remaining underwater than transitioning into travelling or resting, regardless of month (Figure 10). However, there seemed to be a difference in the probability that a whale transitioned from underwater to travel, and from underwater to rest (Figure 10). Whales in November had a 20% probability to start travelling at the surface after being underwater, whereas whales in January did not start travelling at all. Whales that were underwater in November had a 12.5% chance of transitioning to rest, while whales in January had a 34.4% chance to transition to rest; however, there was no significant difference found between these probabilities (Welch Two Sample t-test: t-statistic = 1.4; df = 5.0; p = 0.2).

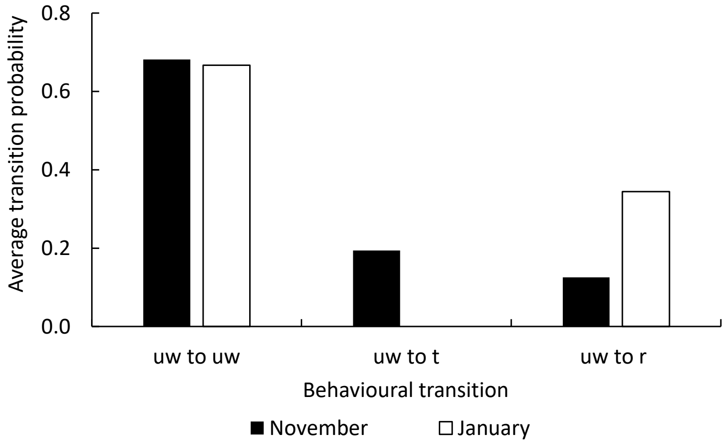

Figure 10. Average transition probability of a west coast right whale that is underwater (uw) to remain underwater, to travel (t) or to rest (r) within fieldwork seasons in November 2022 and January 2023 (N = 7 focal follows; 2022: N = 4; 2023: N = 3).

2.5 DISCUSSION

Southern right whales present on the South African west coast

Results of this study found that adult females with an associated calf seem to make up most of the whales present on the South African west coast. However, this may be different across seasons, given that all females with an associated calf were observed in October (when the annual southern right whale aerial survey is conducted (Best 1990)) to November (this study), but only unaccompanied adults were observed in January 2023. This suggests that some nursing females may use the west coast to accumulate energy reserves prior to initiating their migration to high latitude feeding grounds. Whether this movement is associated with feeding activities, and thus an opportunistic feeding stop in the productive SBUS (as may be the case for HBWs; see Findlay *et al.* 2017), remains to be determined. Also, some cow/calf pairs have only ever been observed on the west coast, which may imply that some calves are born on the west coast, outside of their main calving area on the south coast (Elwen and Best 2004b, 2004a). Given the size of the existing national southern right whale catalogue, length of sighting history data (43 years), and the strong focus of the annual aerial surveys on females with calves (Best 1990) it can be assumed that a good portion of the animals for which no match was found relate to either young individuals or males.

Prey

Results of the prey sampling was in line with the study of Bode-Dalby *et al.* (2023) who found that small copepods, as well as copepods of the Family Calanidae, Centropagidae, and Metridinidae dominated calanoid copepod communities in the SBUS. Small copepod dominance is not a new phenomenon; indeed, the shift from large – to small copepod dominance was already noted in the 1980's in the region (Verheye *et al.* 1998, 2016).

D'Agostino *et al.* (2016) suggested that large calanoid copepods, specifically *Calanus australis*, play a major role in the diet of right whales feeding opportunistically at their Península Valdés calving ground, as it dominates discrete patches of the available prey in the region. Also, bowhead whales (*Balaena mysticetus*) and North Atlantic right whales (*Eubalaena glacialis,* NARW) have been found to mainly target calanoid copepods (Laidre *et al.* 2007; Pomerleau *et al.* 2011; Walkusz *et al.* 2012). Furthermore, Mayo *et al.* (2001) found that baleen plates are more effective in filtering larger copepods; therefore, small copepods have to be very abundant to have the same caloric benefit as larger copepods. This suggest that even if small copepods are available for right whales, they may not make up the majority of their diet. Considering small and larger Calanidae copepods dominate within the SBUS, it can be assumed that they would be the key prey item for right whales feeding in the SBUS. Considering the Genus *Calanoides* are termed upwelling specialists (Borchers and Hutchings 1986; Peterson and Painting 1990), it may not be surprising that these are the main targeted prey species for right whales feeding on the South African west coast.

Despite a limited sample size, the analysis of faecal material in this study confirms feeding right whales target copepod taxa, as suggested by the great proportion of copepod remains found in their faeces, relative to the proportion found in target hauls. Interestingly, the current study found no trace of euphausiids in the faecal material analysed, even though euphausiids were present in the area the whales were feeding. This result agrees with Townsend (1935), who found that whales feed mainly on copepods north of 40°S. Such a preference may be related to the fact that copepods are more abundant than euphausiids in lower latitudes (Rowntree *et al.* 2008). Meaning that copepods are more likely to be concentrated in prey patches dense enough for effective filter feeding, moreover, wherever krill is scarce, right whales feed on copepods (Rowntree *et al.* 2008).

Copepod mandibles (mandibular gnathobases) are composed of chitin and silica (Sullivan *et al.* 1975) and can be used to identify copepods within faeces to species level (Itoh 1970; Sullivan *et al.* 1975) because they are hard and indigestible (Stone *et al.* 1988; Menéndez *et al.* 2007). However, using faecal material to assess the feeding ecology of planktivorous predators, like whales, has its limitations. If whales feed on soft-bodied prey which are easily digested and leave no trace in faecal samples (D'Agostino *et al.* 2016), then it is possible to underestimate the number of prey species the whales are targeting. So, although the faecal material in this study had no trace of soft-bodied zooplankton taxa ("other"), it should not be assumed that right whales only feed on hard-bodied prey, especially since soft-bodied prey, like ctenophores, have been documented as food items for right whales on the Argentine shelf (Bastida and Rodríguez 2009). Similarly, results suggest whales target both hard-bodied and soft-bodied prey, as indicated by the two highest recorded densities in contemporary target hauls being small, and Calanidae copepods as well as "other" zooplankton taxa (including ctenophores).

Feeding behaviour

Whales were not observed surface feeding in the current study, as opposed to observations made in the period 2004 – 2009 which showed that whales were mostly feeding at, or just below the surface. It is known that right whales adjust their feeding depth based on prey abundance (Baumgartner and Mate 2003; Baumgartner *et al.* 2017), and will feed at, or just below the surface if the prey concentration is highest there (Parks *et al.* 2012). In addition, no associated feeding behaviours, like head nodding or baleen flushing (Mayo and Marx 1990; Werth 2001; Barendse and Best 2014) were observed at the surface in recent years.

Considering their foraging at depth in this period, it is assumed that these prey processing behaviours were also performed at depth, as has been discussed by Simon *et al.* (2009) and van der Hoop *et al.* (2019). Behavioural data thus seem to suggest that there may have been a shift in the distribution of dense prey patches from the surface in the early 2000s, to greater depth in more recent years.

The large standard deviations presented in this study are likely due to sample size, which is recognized to be small, especially those included in behavioural observations, and prey hauls. Future research should aim to increase sample sizes to reduce the size of standard deviation and be able to draw stronger conclusions. Also, in order to compare zooplankton abundance across sampling periods, historic sampling methods were repeated, including the use of a 300micron net during prey hauls. Unfortunately, the use of a net with this mesh size may have led to an underestimation of small copepod abundance, as observed in Bode-Dalby *et al.* (2023). However, it is known that no sampling method will lead to a true abundance estimate for all of the taxa present in the water column (see Owens *et al.* 2013). Therefore, the prey haul methods used in this study are acceptable, despite possible underestimation.

2.6 CONCLUSION

This study presents the first insights into the feeding ecology of southern right whales on the South African west coast by the simultaneous investigation of the component of the population engaged in west coast feeding, which prey species these whales target, as well as their feeding behaviour while doing so. Results showed that a large proportion of right whales on the South African west coast are females with an associated calf. This may suggest some nursing females may use the west coast to accumulate energy reserves prior to their annual migration to higher latitude feeding grounds. This is also seen in telemetry data in which 3 of the 15 nursing females with a satellite transmitter travelled up to the west coast prior to migrating to high latitude feeding grounds (MRI Whale Unit, unpublished data). Results of this study also found that right whales on the west coast mainly target *Calanoides*, a large calanoid copepod which dominates copepod communities in the SBUS. In more recent years, right whales were diving to depth to capture this prey, as opposed to more frequent observations of surface feeding behaviour in the early 2000s, despite *Calanoides* copepods remaining the most abundant zooplankton species in target hauls of both collection periods. This suggests possible changes in the distribution of dense prey patches from shallower, to deeper layers within the water column. However, more research and larger sample sizes are needed to form any firm conclusions.

CHAPTER 3 SOUTHERN RIGHT WHALE QUANTITATIVE FEEDING BEHAVIOUR

3.1 ABSTRACT

Southern right whales (*Eubalaena australis*) are faced with high drag caused by opening their large mouths to filter prey, as well as the challenge of remaining within aerobic limits during feeding dives. Feeding at depth therefore requires high energetic investment to perform successfully, but at the same time can present whales with high energy return. To gain some insight into this, this study presents a quantitative assessment of southern right whale feeding behaviour measured using animal-borne biologging tags, equipped with a camera (Customized Animal Tracking Solutions). Moreover, the tags used in this study have not previously been used to assess southern right whale feeding behaviour. Therefore this study provides novel insights into southern right whale feeding behaviour. Results showed that right whales alternated the depth at which they were feeding, suggesting they are able to adjust their foraging strategy over small spatial and temporal scales. Data further showed that right whales on the South African west coast had comparable feeding bout duration and speed to other Balaenids, and seemed to increase foraging time with increasing depth presumably to optimise the trade-off between energy expenditure and uptake. Due to a limited sample size, extrapolating the results of this study to right whale feeding behaviour in high latitude feeding grounds is not recommended. Nonetheless, the study represents the first steps into investigating quantitative right whale feeding behaviour in a low latitude feeding ground.

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3.2 INTRODUCTION

Due to their gigantic size, aquatic lifestyle and carnivory, southern right whales (*Eubalaena australis*, right whales) have high metabolic rates (Lockyer 1981; Williams *et al.* 2001; Williams 2006) and they feed on prey that are extremely small to meet their metabolic needs (Domenici 2001). They also require that their prey be concentrated into patches of high density in order to filter feed effectively (Wishner *et al.* 1995). How they find this resource on large scales is not understood, however, there are some suggestions, including echolocation or listening for prey noises (Hamner *et al.* 1988). On smaller scales, right whales find discrete prey patches at all levels of the water column by using tactile senses, in the form of sensory hairs around their mouths, which bend when they are struck by prey that are in close proximity (Payne 1976; Baumgartner *et al.* 2007; Kenney *et al.* 2020). As a result, they make course adjustments during feeding, as it ensures that they remain feeding in the place of highest prey concentration within a patch (Mayo and Marx 1990; Baumgartner *et al.* 2017; Kenney *et al.* 2020). Indeed, the extreme rate at which right whales accumulate lipid reserves during foraging testifies to their ability to find and feed on dense patches of prey (Brodie 1975; Williams *et al.* 2013).

Baleen whales, like right whales, differ from most mammals by a remarkable morphological adaptation: within their mouths are 200 – 260 baleen plates, instead of calcified teeth, that they use to capture their prey (Diedrich 2013). The anatomy of baleen whales has been studied for over a century, but investigations about the mechanisms behind baleen whale foraging is comparatively modern (Eschricht and Reinhardt 1866; Pyenson *et al.* 2012; Goldbogen *et al.* 2013a). Unlike rorqual whales that lunge feed, right whales use continuous ram filter feeding (Goldbogen *et al.* 2013b). They also do not trap, ambush or herd their prey, but are entirely dependent on the environment to concentrate their prey into dense patches (Baumgartner *et al.* 2007). Therefore, right whale foraging has been likened to oceanic grazing (Hazen *et al.* 2015).

Whether at depth, or at the surface, right whales propel themselves through the water with their mouths open, exposing their baleen plates in order to filter feed (Watkins and Schevill 1979; Werth 2001; Lambertsen *et al.* 2005; Goldbogen *et al.* 2017b; Potvin and Werth 2017). Right whale baleen acts as a cross flow filtration system, slowing prey-filled water down in the mouth as it washes over the plates in parallel, thereby concentrating small prey items so that they may be swallowed (Potvin and Werth 2017). Specifically, the edge of the plates that face the inside of the mouth has fibres which intertwine to create a dense mat that filters prey (Pivorunas 1979; Fudge *et al.* 2009; Goldbogen *et al.* 2017b) and enables right whales to only capture organisms of a certain size (Diedrich 2013). An implication of cross flow filtration is that prey will not clog the baleen, which negates the need for mechanistic prey processing, like removing prey from the baleen using the tongue (Goldbogen *et al.* 2017b). Instead, right whales seem to pause filter feeding momentarily while they process (swallow) prey at depth allowing them to resume filtering without returning to the surface (Simon *et al.* 2009; van der Hoop *et al.* 2019).

What is known of South African right whale foraging derives from whaling records in the 19th and 20th-centuries (IWC 2001), observing feeding behaviour near shore (Hamner *et al.* 1988; Barendse and Best 2014; Calderan *et al.* 2023), transect surveys in the Southern Ocean (Reilly *et al.* 2004) and satellite tagging (Mate *et al.* 2011; Zerbini *et al.* 2015; Best and Mate 2023). The population likely has important feeding grounds at the Subtropical Convergence, and the Polar Front (Mate *et al.* 2011), as well as off the coasts Tristan Da Cunha and Bouvet Island (Best and Schell 1996; Mate *et al.* 2011). In addition, the South African west coast is known as a feeding ground for this population where whales have been observed feeding at the surface or at depth (IWC 2013; Barendse and Best 2014).

Observing right whale feeding at, or just below the surface, often leads to an underestimation of feeding behaviour, especially if visibility is poor (Fortune *et al.* 2020). Right whale feeding at the surface might also be disturbed by approaching research vessels (Fortune *et al.* 2020). Moreover, the inability to study whale feeding behaviour at depth (Goldbogen *et al.* 2013a) led to the use of animal-borne biologging tags to measure small-scale movements during feeding (Nowacek *et al.* 2001; van der Hoop *et al.* 2017). These tags also place feeding at depth in context of energy expenditure and prey acquisition (Gleiss *et al.* 2011; Goldbogen *et al.* 2012).

Data from biologging tags have provided much insight into bowhead whale (*Balaena mysticetus*) and North Atlantic right whale (*Eubalaena glacialis*, NARW) foraging. For example, 1) how they reduce drag generated by filter feeding, 2) what small-scale adjustments are made during foraging, 3) at what depths they are able to feed while remaining within aerobic limits and 4) how they maximize foraging at depth (Werth 2004, Simon *et al* 2009; van der Hoop *et al* 2019). This study provides novel insights into southern right whale feeding on the South African west coast through the assessment of feeding behaviour using biologging tags.

3.3 MATERIALS AND METHODS

Fieldwork

In January 2023, short duration (< 24hr), animal-borne biologging tags were deployed on three adult right whales in Yzerfontein (33°20' S, 18°8' E), located north of Cape Town with an approximate water depth of 150m (Figure 1). The tagged whales were confirmed as three different individuals by means of photo-identification using unique callosity patterns (Payne *et al.* 1983). Whales were approached on a 6m semi-rigid inflatable boat with the tags (Customized Animal Tracking Solutions; see Goldbogen *et al.* (2017a), www.cats.is) placed at the end of a carbon-fiber pole. The tags were deployed and attached to the whales' backs with four suction cups. Once the suction failed, the tags floated on the sea surface and were retrieved using VHF telemetry. Deployments occurred over two days: the first tag was deployed on 16 January, and the other two were deployed on 20 January. The tags used had built in accelerometers (400Hz), magnetometers (50Hz), gyroscopes (50Hz), pressure and temperature sensors (10Hz), GPS, a video camera, and a hydrophone. Also, since the tags were archival tags, the recorded and stored data could only be downloaded after tag retrieval.

Figure 1. The study area indicating the locations where 3 adult right whales were tagged with biologging tags offshore of Yzerfontein (circles). The study area is located north of Cape Town, on the west coast of South Africa as shown by the insert.

Data analyses

Raw data were processed by Dr P. Segre and Dr M. Savoca (Stanford University) as part of the collaborative nature of this study. This processing entailed aligning the accelerometer and magnetometer signals to the body axis of the whale, and removing tail stroke sampling errors with a low-pass filter (Johnson and Tyack 2003; Segre *et al.* 2016). These processed data were then used in this study to calculate the depth (meters), pitch (degrees), roll (degrees) and speed (meters per second) of whales during the deployments (Johnson and Tyack 2003). Speed measurements were calibrated using dives (depth: ~ 30 – 40m, pith: 30deg) (Cade *et al.* 2017). All statistical analysis were done in R 4.3.1 (R Core Team, 2023).

Feeding incidents, defined as times where whales opened their mouths presumably to feed, were identified using video data recorded by the biologging tags (from now on referred to as “tags”). These feeding incidents were identified in both tagged, and non-tagged whales (which swam past the tagged whale and were therefore in view of the tag camera). From these incidents, a feeding bout was defined as a period of time that started when the whale’s mouth opened and ended when the whale’s mouth closed. These feeding bouts occurred either close to the surface (< 20m) or at depth (> 20m) and were marked by clear views of the bottom lip, visible either right or left of the top lip, with a prominent gap between the lips (see example Figure 2 a, b). After identifying feeding incidents and feeding bouts, the depth, speed, pitch, and roll of the tagged whales were measured and analysed. Also, since non-tagged whales were in view of the tag camera (thus at the same depth as the tagged whales), the depth was also measured for the observed feeding incidents of non-tagged whales.

In some cases, the exact moment of mouth closure was not clearly visible, due to 1) the body obscuring the head and lips, 2) the tag camera facing away from the head, 3) the non-tagged whale disappearing out of frame with its mouth still open and 4) the water was too dark to see the head or lips. Therefore, not all feeding incidents could be defined as feeding bouts. Both feeding incidents, and feeding bouts occurred during so called “feeding dives”. During a feeding dive, the whale descended below the surface, opened its mouth to feed, and then ascended back to the surface (Figure 2 a, b).

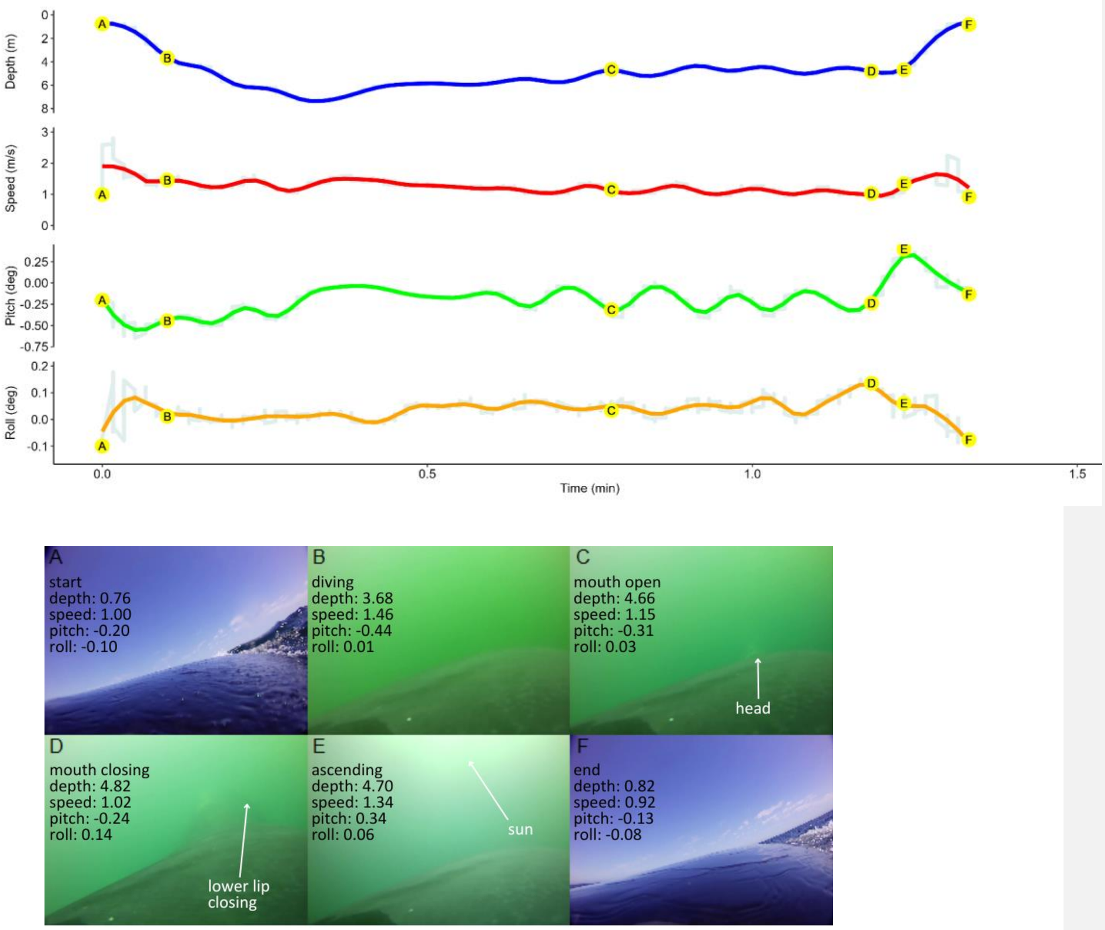

Figure 2a. Dive profile from deployment B, including one feeding bout (t = 55.8sec), with key moments also pictured in the photograph labelled A – F. A smoothed line was applied to the data (colour), on top of the raw data (light grey). A) whale at the surface before diving, B) whale diving, C) mouth open, note the upward angle of the top lip with the callosity visible, D) mouth closing with the lower lip visible to the right of the top lip, E) mouth closed, note that the head is no longer visible, compared to C, F) whale ascending to the surface.

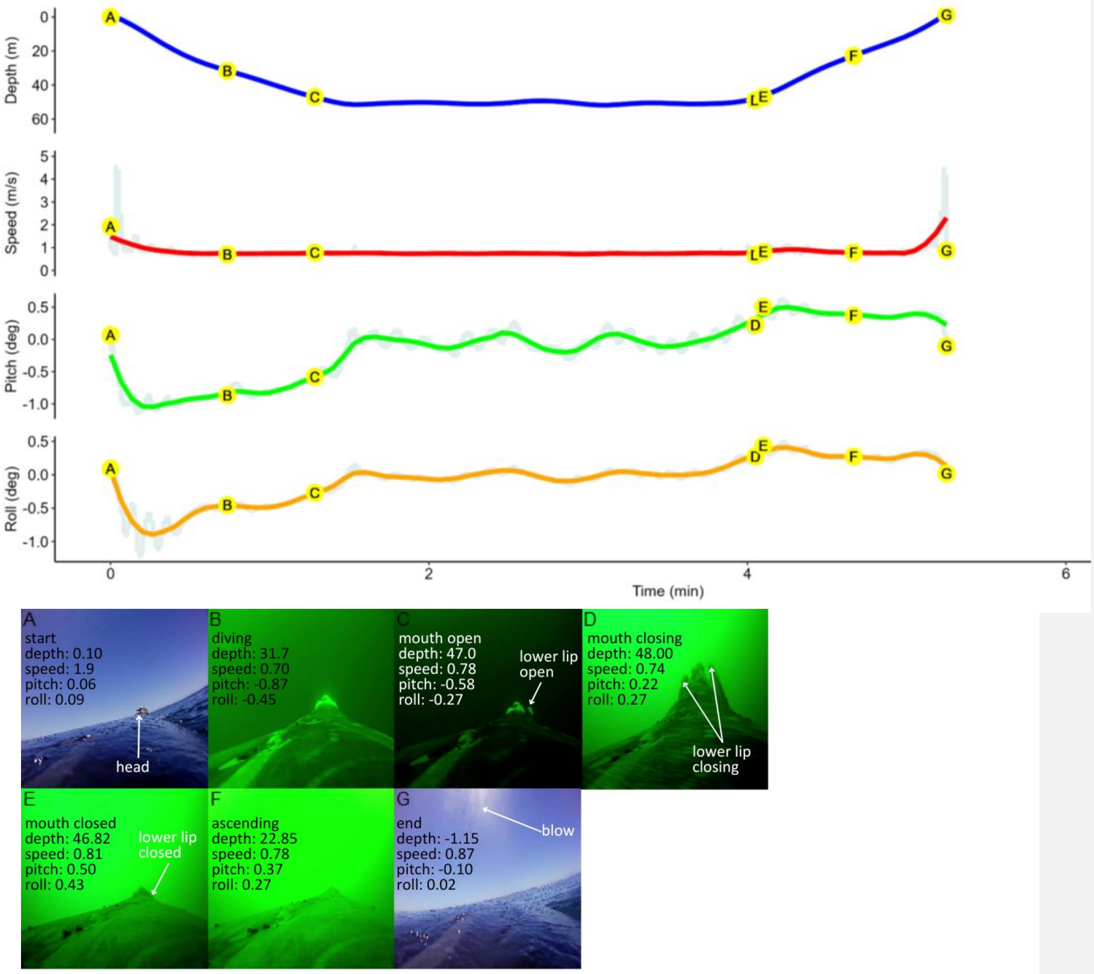

Figure 2b. Dive profile from deployment C, including a feeding bout (t = 2.8min), with key moments also pictured in the photograph labelled A – G. A smoothed line was applied to the data (colour), on top of the raw data (light grey). A) Whale at the surface before diving, B) whale diving to depth, C) mouth open, note the gap between the lower lip and the top lip, D) mouth closing with the lower lip visible right and left of the top lip, E) mouth closed with no gap between lower and top lip, F) whale returning to the surface, note the light green colour of the water as the whale is turned towards the sun at the surface, compared to the darkness in B when the whale was turned away from the sun while diving, G) whale blows at the end of the feeding dive at the surface.

3.4 RESULTS

A total of 11hrs 59min of video data, recorded during the daytime, were analysed from tag deployments on 3 different whales (confirmed by photo-identification data). In these data, 79 feeding incidents could be observed. However, only 33 of these incidents were defined as feeding bouts due to clear observation of the time of mouth opening and closure. All feeding incidents combined amounted to 2hrs 20min of video data, with feeding bouts accounting for 56min of these. Almost all feeding bouts (except for five) occurred during a single feeding dive; therefore, it seems most feeding dives only included one feeding bout.

Summary of deployments

Deployment A

A total of 4hrs 35min of video data (Table 1) were analysed for deployment A; however, due to the angle of the tag, and consequent direction of the camera, attaining measurements of feeding bouts for the tagged whale was not possible (i.e., the whale's head was out of frame for the entirety of the video data). However, this deployment allowed for the identification and depth analysis of five feeding incidents of non-tagged whales, but none of these incidents could be defined as feeding bouts due to the inability of seeing the whales closing their mouths.

Deployment B

During the 4hrs 29min of video data (Table 1) analysed for deployment B, 59 feeding incidents were recorded, of which 27 could be defined as feeding bouts.

Deployment C

There were 2hrs 54min of video data for deployment C (Table 1), during which the tag moved onto the flipper of another whale for 1hr 50min (Figure 3). Although video data still allowed the identification of feeding incidents and bouts at this time, the speed, pitch, and roll data during these incidents and bouts could not be included in the final analysis due to the movement of the flipper limiting accurate measurement of these parameters. In total, 15 feeding incidents were recorded in this deployment, including 6 feeding bouts.

Table 1. The total time video data analysed, as well as the number of feeding incidents and feeding bouts recorded in deployments A, B and C. Also included are the number and duration of all recorded feeding incidents and feeding bouts per deployment.

Deployment	Video time analysed (total time hrs)	Number of feeding incidents (total time hrs) N = 79	Number of feeding bouts (total time min) N = 33
A	4hrs 35min	5 (0hrs 2min)	0 (0min)
B	4hrs 29min	59 (1hr)	27 (26min)
C	2hrs 54min	15 (2hrs 20min)	6 (30min)

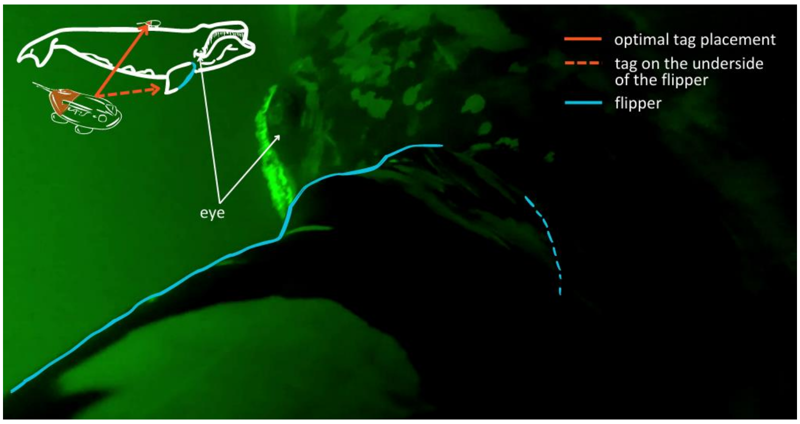

Figure 3. Video screenshot of deployment C showing the tag on the flipper of another whale. The graphic shows the optimal tag placement needed to reliably measure the speed (m/s), pitch (deg) and roll (deg) of the whale.

Feeding incidents

Depth of feeding incident ranged between a minimum of 0.6m (deployment B) and maximum of 61.5m (deployment C) (Figure 4). The average depth of a feeding incident for deployments A and C were 42.8m (± 6.7) and 44.9m (± 13.6) respectively, compared to 5.0m (± 2.8) for deployment B.

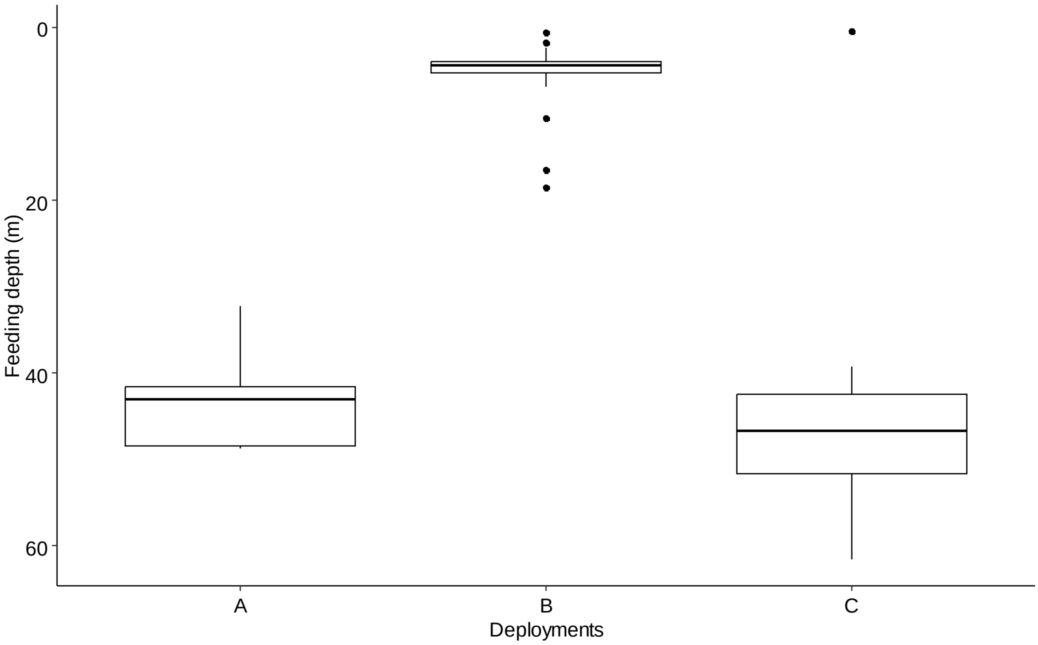

Figure 4. The depths (m) at which feeding incidents occurred in deployments A, B and C. Number of feeding incidents (N = 79), with deployments (A: N = 5; B: N= 59; C: N = 15). Black lines indicate median depth, and vertical lines indicate minimum and maximum depth. Outliers are indicated with a black dot.

The average instantaneous speed (m/s) – the swimming speed at the start of a feeding incident – was 1.13m/s (± 0.2) for deployment B and 1.2m/s (± 1.0) for deployment C (Figure 5). Deployment A was not included, because every feeding incident recorded during this deployment was of non-tagged whales; therefore, the speed that these whales were swimming at could not be measured by the tag and was therefore not included in this analysis.

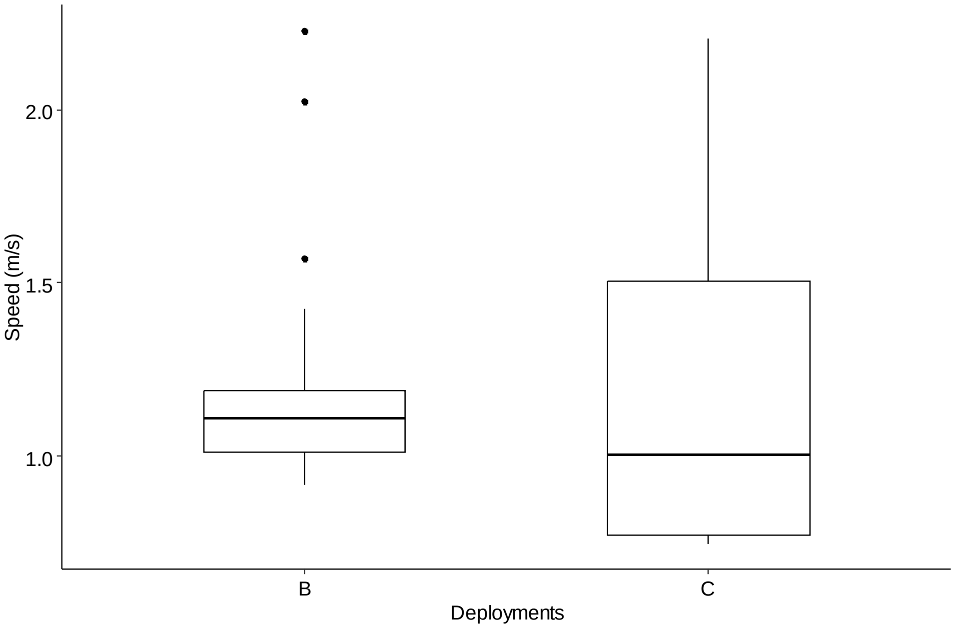

Figure 5. The swimming speed (m/s) of whales at the start of a feeding incident in deployment B and deployment C. Black lines indicate median speed, and vertical lines indicate minimum and maximum speed. Outliers are indicated with a black dot.

Instantaneous speed in shallower feeding incidents were similar to those at deeper feeding incidents, and no clear trend could be found (Figure 6).

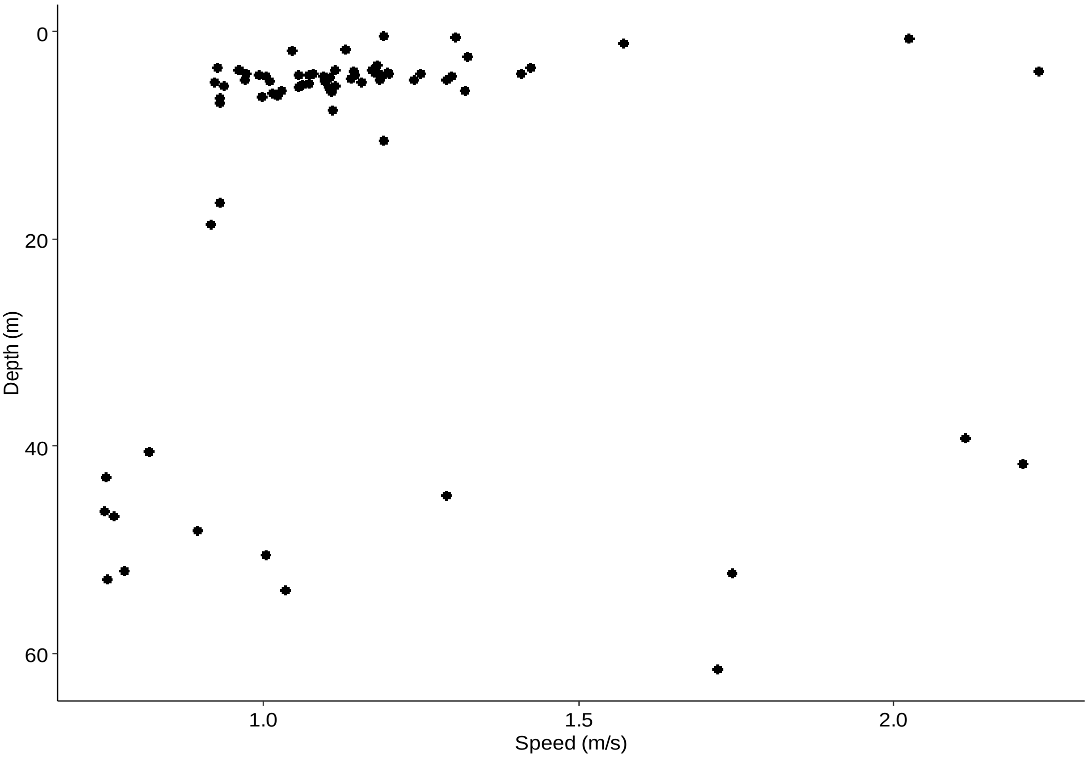

Figure 6. The depth (m) and instantaneous speed (m/s) of whales at the start of a feeding incident in deployment B and C (N = 71; B: N = 59; C: N = 15).

Feeding bouts

Feeding bout duration ranged between 3.6sec (deployment B) and 4.7min (deployment C). On average, deployment B had a shorter bout length (51.6sec ± 0.6) than deployment C (2.6min ± 1.6) (Figure 7).

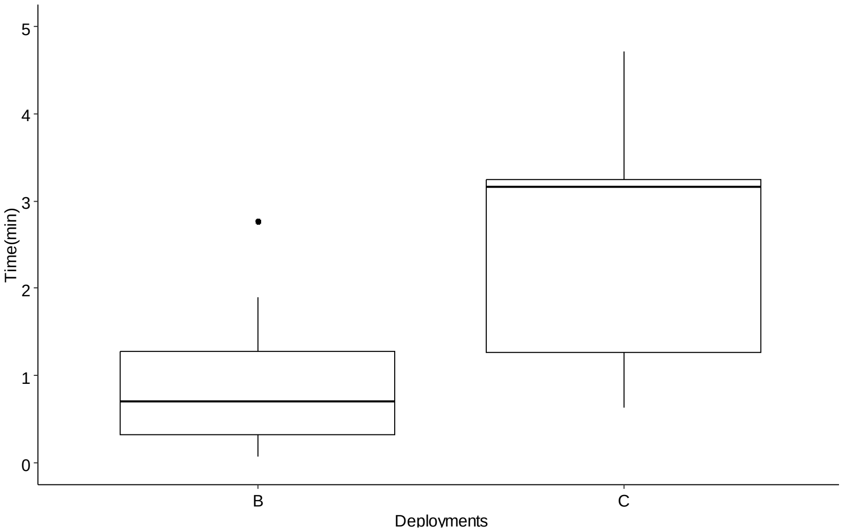

Figure 7. The feeding bout length (min) measured during deployments B and C (N = 33; B: N = 27; C: N = 6).

Average swimming speed seemed to differ between bout length groups (H (4) = 141.9, p < 0.001; Table 2). Pairwise comparisons using Dunn's test showed that speed within groups 4 and 5 were significantly different from those of groups 1, 2 and 3 (p < 0.001), as well as between groups 4 and 5 (Figure 8).

Table 2. The bout length (t = min), and speed (m/s) of whales during feeding bouts in deployments B and C.

Bout length group	Bout length (min)	Mean speed (m/s) ± SD
1	t < 1	1.1 ± 0.2
2	1 ≤ t < 2	1.0 ± 0.1
3	2 ≤ t < 3	1.1 ± 0.1
4	3 ≤ t < 4	0.7 ± 0.03
5	4 ≤ t < 5	1.5 ± 0.2

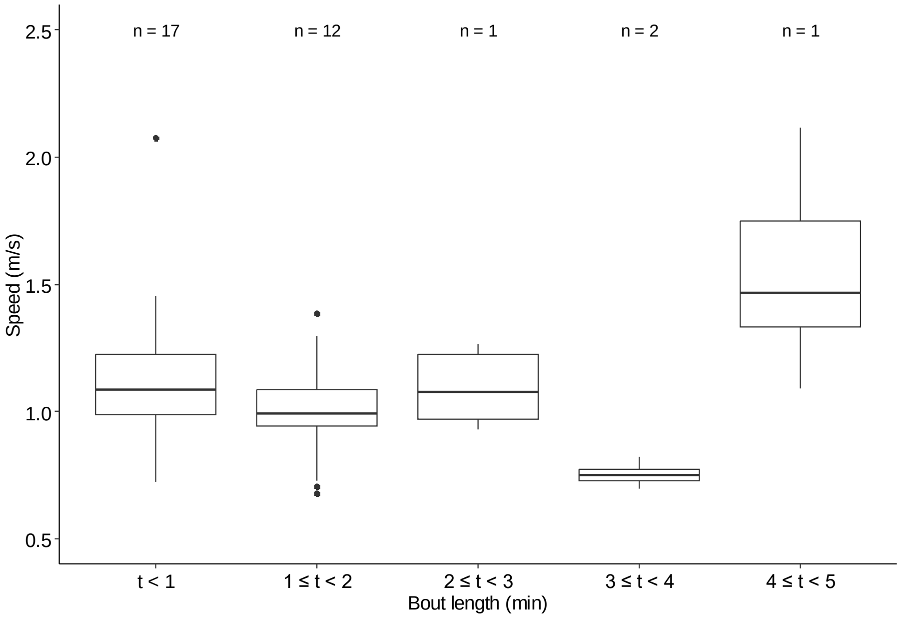

Figure 8. The speed (m/s) of whales during feeding bouts (N = 33). The bout length is separated into 5 groups, with t = time (min), with the number of feeding bouts above every bout length group.

There seemed to be a difference in the depth that whales were feeding at between bout lengths that lasted less than 3min, and bout lengths that lasted longer than 3min (Figure 9). Results showed that there were differences in depth between bout length groups (Kruskal-Wallis: H (4) = 138.8, $p < 0.001$). Specifically, groups 1, 2 and 3 were all significantly different from groups 4 and 5 (Dunn's test: $p < 0.001$). Results also showed that there was a significant positive relationship between average depth and bout length (Pearson correlation coefficient = 0.7; linear regression: (F (1, 32) = 23.8, $p < 0.001$)).

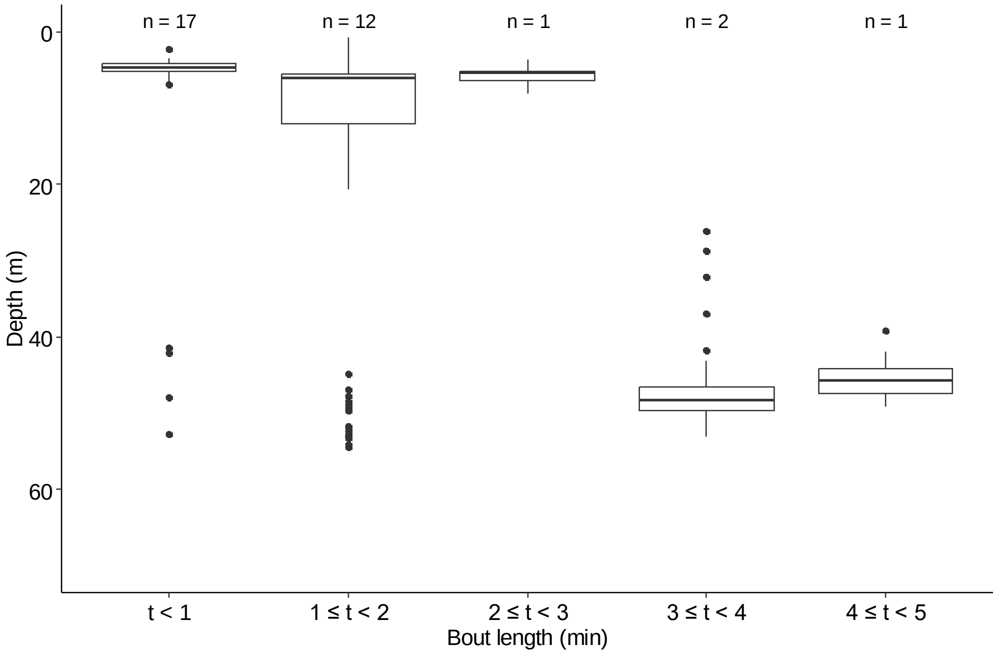

Figure 9. The depth (m) of whales during feeding bouts of different duration (N = 33). The bout length is separated into 5 groups, with t = time (min), with the number of feeding bouts above every group.

The average swimming speed during feeding bouts seemed to decrease slightly with increasing bout depth (Figure 10). Results showed that there was a significant difference in average swimming speed between bout depth groups (Kruskal-Wallis: H (6) = 69.6, $p < 0.001$), with significant differences between group 1 and groups 3, 5, 6 and 7 (Dunn's test: $p < 0.001$). The same test also revealed that group 6 and 7 differed significantly from all groups, except group 3 ($p < 0.001$) (Table 3).

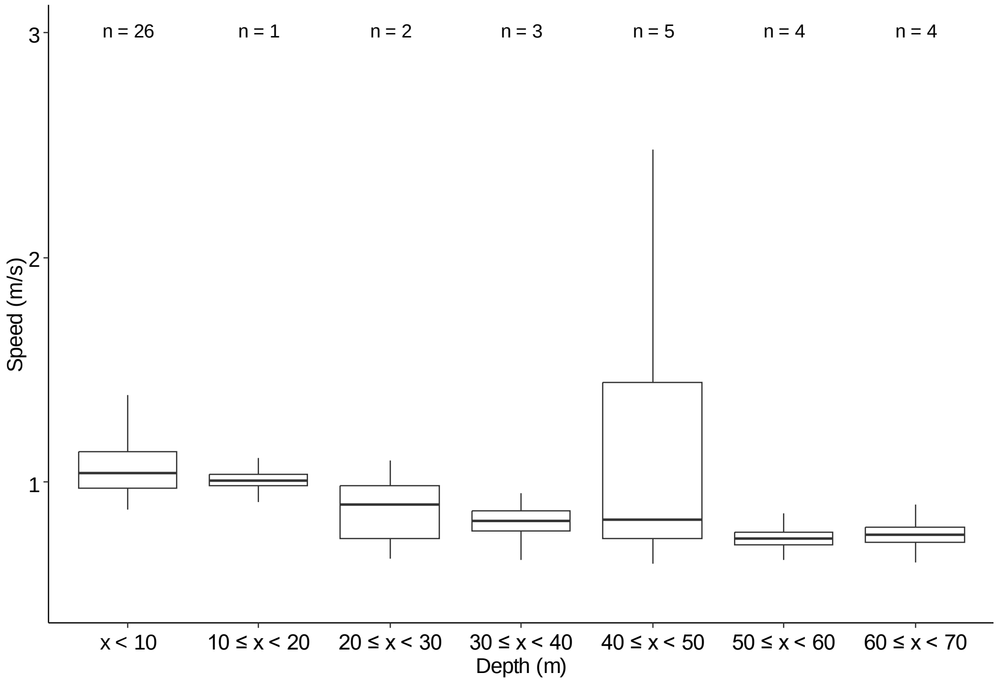

Figure 10. The speed (m/s) of right whales during feeding bouts (N = 33) at 7 depth groups. The depth during some feeding bouts had a wide enough range to be included in more than one depth group. Specifically, 1 feeding bout of deployment B was included in more than one depth group, while all 6 feeding bouts of deployment C were included in at least 2 depth groups.

Table 3. The average swimming speed (m/s) of whales during feeding bouts at different depths (m) in deployment B and C.

Bout depth group	Depth (m)	Mean speed (m/s) ± SD
1	$x < 10$	1.1 ± 0.1
2	$10 \leq x < 20$	1.0 ± 0.1
3	$20 \leq x < 30$	0.8 ± 0.1
4	$30 \leq x < 40$	0.8 ± 0.3
5	$40 \leq x < 50$	1.1 ± 0.4
6	$50 \leq x < 60$	0.7 ± 0.1
7	$60 \leq x < 70$	0.7 ± 0.1

3.5 DISCUSSION

Filter feeding in baleen whales occurs throughout the water column (Baumgartner *et al.* 2003; Simon *et al.* 2009; Parks *et al.* 2012); however, feeding at depth is notoriously difficult to observe directly (Goldbogen *et al.* 2013a). Luckily, movement, audio and video sensors built into animal-borne biologging tags have allowed for the quantification of feeding behaviour of baleen whales (Simon *et al.* 2009, 2012; Aoki *et al.* 2012). The use of such tags in this study have been useful in providing the first insights into right whale feeding on the South African west coast.

Horizontal movement

Dive profiles, as displayed in Figure 2 a, and b, can make it seem that a whale is moving in one straight, horizontal line during feeding dives (van der Hoop *et al.* 2019). In reality, whales make fine-scale adjustments in the horizontal and vertical plane based on variation in prey density (Mayo and Marx 1990; Baumgartner *et al.* 2017; Kenney *et al.* 2020). The two dive profiles presented here resemble the typical right whale feeding dives defined in Baumgartner and Mate (2003), during which right whales maximized the time they spent feeding at depth.

Results of this study revealed that a single feeding bout (periods between the whale’s mouth opening to feed, and closing again) was observed per feeding dive. This is interesting as studies on bowhead whales and NARWs revealed that there can be multiple feeding bouts within a single feeding dive where whales halted feeding momentarily, in a consistent manner, to swallow prey at depth (Simon *et al.* 2009; van der Hoop *et al.* 2019). Due to the accumulation of prey in the mouth it seems that swallowing at depth might be necessary (van der Hoop *et al.* 2019), and negates the need for baleen flushing or removal of prey by the tongue (Werth 2001; Goldbogen *et al.* 2013b). Since pauses in right whale feeding (therefore multiple feeding bouts within a single dive) could not be detected here, it may point to prey patches at depth not being dense enough to warrant swallowing of accumulated prey within single dives. However, the current study did not investigate prey density and abundance in the area at the times the whales were tagged, limiting conclusions.

Bowhead whales feed for 2.4min, and NARWs for about 50sec, respectively (Simon *et al.* 2009; van der Hoop *et al.* 2019). This study found that right whales had average feeding bout lengths between 50sec – 5.0min, suggesting that right whale feeding bout length is similar to those of other Balaenids.

Vertical movement

For whales, the metabolic cost of diving is pinned against the potential benefit that can come from acquiring prey at depth (Goldbogen *et al.* 2013b). If denser patches are usually found at depth, compared to less dense, low quality prey patches which tend to be shallower (Hazen *et al.* 2015; Friedlaender *et al.* 2016), then there is a benefit to diving, especially if prey patches in shallower waters fall below the density threshold that makes the prey patch worth feeding in (Goldbogen *et al.* 2011). To maximize foraging at depth, baleen whales should then take full advantage of their aerobic capacity underwater by spending most of the dive time feeding (Thompson and Fedak 2001). This study showed that the tagged right whales seemed to have longer bout lengths as feeding depth increased, suggesting that whales at depth were maximizing energy gain by feeding for longer periods (Acevedo-Gutiérrez *et al.* 2002). In turn, this may mean that more time is required at the surface to rest and recover between dives (Acevedo-Gutiérrez *et al.* 2002). However, Fortune *et al.* (2020), found that the time bowhead whales took to recover at the surface did not increase with dive duration or depth, suggesting that bowhead whales operate within their aerobic limits when diving between depths of 10 – 305m. Also, NARWs remained within aerobic limits when diving to around 120m (Baumgartner and Mate 2003; Baumgartner *et al.* 2017). Since closely related right whales in this study had feeding depths between 5 – 70m, they are also likely operating within their aerobic dive limits and would not need more recovery time after deeper, longer dives compared to shallower, shorter dives. Therefore, although diving to, and remaining at depth is energetically costly, it is highly beneficial, especially since it may not necessarily lead to increased surface intervals.

Results of the current study further showed that whales were feeding at different depths in the water column, which is not surprising since prey density varies within patches and determines the depth at which whales will feed (Baumgartner and Mate 2003; Michaud and Taggart 2011; Baumgartner *et al.* 2017). Moreover, right whales in this study seemed to feed either in a shallower layer (0 – 20m) or a deeper layer (30 – 70m), indicating that prey is available to the right whales both near the surface and at depth. Similarly, bowhead whales appeared to alternate between foraging at depth and in shallower waters (Laidre *et al.* 2007; Fortune *et al.* 2020). However, unlike bowhead whales and NARWs, the tagged whales were not feeding deeper than 100m, despite it being possible within the area (water depth approximately 150m).

Speed during feeding

Whether at the surface, or at depth, right whales need to open their mouths and expose their baleen plates in order to filter feed (Watkins and Schevill 1976; Werth 2001; Lambertsen *et al.* 2005; Goldbogen *et al.* 2017b; Potvin and Werth 2017). While doing so, they will experience a considerable amount of drag generated through filtering (Nowacek *et al.* 2001; Werth 2001, 2004). For related bowhead whales, this drag can be up to 6 times more than what they experience while swimming with their mouths closed (Simon *et al.* 2009), and about 5 times more for NARWs (Nousek-McGregor 2010). To both reduce drag (thereby conserving energy) and oxygen consumption, both bowhead whales and NARWs swim slowly when feeding (Werth 2004; Simon *et al.* 2009; van der Hoop *et al.* 2019). Bowhead whales swim at an average speed of 0.75m/s while feeding (Simon *et al.* 2009), while NARWs swim faster at 1.2m/s while feeding (van der Hoop *et al.* 2019). Results in the current study are comparable to this, as right whales swam between 0.5 – 2.3m/s while feeding.

Results showed that whales swam faster during longer feeding bouts. Oxygen is the main factor that limits foraging endeavours at depth, since whales need sufficient oxygen stores to sustain dives while remaining in tolerable limits of oxygen depletion (Goldbogen *et al.* 2013b); simply put, whales can only dive so long before they need to return to the surface to breath. Results therefore suggest that whales may swim faster during longer feeding bouts so that they could capture as much prey as possible before they had to return to the surface. On the other hand, results of this study suggest that the tagged right whales had slower swimming speeds when feeding at depth, compared to feeding in shallower waters. Whales will expend energy to reach prey patches at depth, since they must overcome positive buoyancy by using powerful fluke strokes (Nowacek *et al.* 2001; Baumgartner and Mate 2003). Therefore, it is expected that diving to deeper prey patches would require more energy than diving to shallower prey patches, possibly resulting in slower swim speeds at greater depth to conserve energy (Nowacek *et al.* 2001; Werth 2001, 2004).

It is however important to acknowledge some limitations to this study. Firstly, a small sample size means it cannot be assumed that the captured behaviours apply to all right whales feeding on the South African west coast. For example, we did not observe skim-feeding at the surface in the video footage, although right whales are known to surface feed on the west coast (Barendse and Best 2014). Secondly, larger krill schools seemed to result in longer dives, and regular surface intervals in right whales feeding in the Antarctic (Hamner *et al.* 1988). However, since this study limited its analysis to feeding bouts and did not investigate feeding dive length, conclusions could not be drawn between feeding dive length and prey density and abundance. Moreover, acknowledging the simultaneous analysis of feeding behaviour at depth and prey distribution, abundance and behaviour is a more robust approach in understanding the complexity surrounding right whale feeding and their environment (Croll *et al.* 1998, 2005), it was not possible in this study. Lastly, although using accelerometer vibrations to measure speed is most accurate compared to other sensors (Cade *et al.* 2017), the speed measurements of these accelerometers have high variation when whales are moving slower. The right whales in this study were feeding at slow speeds therefore any interpretations regarding speed should be made with caution.

3.6 CONCLUSION

Results of this study showed that right whales alternated between feeding on prey in deeper and shallower patches, while maximizing prey uptake regardless of depth, suggesting they may be able to adjust their foraging strategy over small spatial and temporal scales. This study further showed that right whales on the west coast had comparable feeding bout duration and speed to other baleen whales in their feeding grounds (Simon *et al.* 2009; van der Hoop *et al.* 2019) and seem to maximize prey uptake by increasing foraging time at depth (Baumgartner and Mate 2003), as well as in shallower waters by increasing foraging speed. This study represents the first steps into quantitatively investigating right whale feeding behaviour in a low latitude feeding ground. However, due to a limited sample size, extrapolating the results of this study to right whale feeding behaviour in their offshore feeding grounds is not recommended. Further studies on the feeding behaviour of right whales on the South African west coast using biologging tags is highly recommended.

CHAPTER 4 GENERAL DISCUSSION AND CONCLUSIONS

4.1 OVERVIEW OF KEY FINDINGS

The overall aim of this study was to investigate the feeding ecology of right whales feeding on the South African west coast in the vigorously productive environment of the Southern Benguela Upwelling System (SBUS).

The first data chapter (chapter 2) analysed photo-identification data, prey hauls conducted at fixed stations and near presumed feeding whales, and qualitative behavioural observations. The results revealed that most of the individuals present on the west coast of South Africa are adult females with associated calves. This result may indicate that females use the west coast for some opportunistic feeding prior to migrating south to their high latitude feeding grounds. This is in line with telemetry data (MRI Whale Unit, unpublished data). In addition, some cow/calf pairs were never observed on the south coast, prior, or after an initial identification on the west coast. This may imply that some calves of the South African population are born on the west coast, outside their main calving ground (on the south coast between Walker Bay and St Sebastian Bay (Elwen and Best 2004b, 2004a). Results further showed that when feeding on the west coast, right whales mainly targeted large calanoid copepods (specifically *Calanoides*).

The second data chapter (chapter 3) focused on quantitively describing feeding behaviour by using animal-borne biologging tags that measured the speed, pitch, roll and depth of whales during feeding. Results from this chapter revealed that right whale swimming speed during feeding, as well as their feeding bout length is similar to other ram filter feeding baleen whales (Balaenids). Results also showed that the tagged right whales alternated between feeding in shallower and deeper prey patches, showing that they are able to exploit dense prey patches regardless of changes to prey density over space and time. In addition, the tagged right whales seemed to maximize their prey uptake by increasing foraging time at depth, but were also maximizing prey uptake in shallower waters by increasing foraging speeds. This speaks to the versatility of right whale feeding over small temporal and spatial scales.

4.2 IMPLICATIONS

Right whales show high fidelity to their feeding grounds (Best 2000; Valenzuela *et al.* 2009; Carroll *et al.* 2020), to which they return after migrating to their calving grounds every year (Cummings 1985). Feeding ground locations are taught to calves by mothers via vertical cultural transfer during extended parental care

(Rendell and Whitehead 2001; Whitehead *et al.* 2004). However, if individuals are taught to return to the same feeding ground, and no innovation occurs within a population to uncover new feeding grounds, right whales may be caught in an ecological trap whereby individuals return to feeding grounds that have deteriorated in prey quality due to climate change impacts (Schlaepfer *et al.* 2002; Keith and Bull 2017). Since right whales are capital breeders that use the energy they gain in their feeding grounds to reproduce (Jönsson 1997), a reduction in prey quality in their feeding grounds may lead to a reduced reproductive output. Indeed, nutritional stress has been linked to a lowered reproductive output in right whales (Lockyer 1986; Reeves *et al.* 2001; Greene *et al.* 2003; Hlista *et al.* 2009; Ward *et al.* 2009; Williams *et al.* 2013) and there is growing evidence that the yearly breeding success in right whales is consequently related to global climate signals (Leaper *et al.* 2006; Seyboth *et al.* 2016). It was even suggested that it is quite possible that the calving output, and right whale population dynamics, are sensitive to small changes in oceanographic conditions in the Southern Ocean (Leaper *et al.* 2006).

Also within the South African population of right whales, a recent study has revealed changes in their feeding strategy as well as a shift of feeding efforts equatorward (van den Berg *et al.* 2021). In addition, these changes coincided with a period of slowed population growth (Brandão *et al.* 2018), a reduction in calving rate (Vermeulen *et al.* 2019) and a reduction in physical body condition (Vermeulen *et al.* 2023). Together, these changes strongly point towards environmental change in the high latitude feeding grounds of the population.

The present study revealed that mostly adult female right whales use the South African west coast as a feeding ground. This may be important as lactation is particularly demanding for females (Lockyer 1984; Oftedal 1997); for example, right whale mothers lose, on average, 25% of their body volume during the initial period of lactation (Christiansen *et al.* 2018). Therefore, the SBUS might be important for female right whales that are building up energy reserves to cover the energy required for lactation, as well as their annual migration to their offshore feeding grounds (Hoffmeyer *et al.* 2010). Although the absolute number of right whales foraging on the South African west coast is limited considering the size of the population (50 individuals identified on a catalogue of 2 103 individuals), as the population increases and energy requirements are not met (Vermeulen *et al.* 2023), the importance of the SBUS as a temporary foraging stop should not be underestimated.

The SBUS is a vigorously productive marine ecosystem, where copepods are highly abundant when upwelling occurs during summer months (Hutchings *et al.* 2009; Verheye *et al.* 2016). Although several changes have emerged in the SBUS since the 1980’s, copepod abundance has increased 10-fold, and copepod biomass 100-fold since the 1950’s (Verheye *et al.* 1998; Verheye and Richardson 1998), therefore presenting right whales with an abundance of prey patches to exploit. Although there is some foraging plasticity within the population, the productivity of the SBUS will likely not curb the effects of environmental change in their high latitude feeding grounds (van den Berg *et al.* 2021).

Understanding right whale feeding behaviour, in conjunction with their distribution, abundance and prey behaviour provides a robust understanding of right whale interactions with their environment (Croll *et al.* 1998, 2005; Goldbogen *et al.* 2013b). Moreover, taking advantage of their closeness to the South African coast and ability to conduct coastal fieldwork, will allow for an improved understanding of right whale feeding behaviour and energetics.

4.3 FUTURE DIRECTIONS AND RESEARCH NEEDS

It must be acknowledged that the sample sizes included in this study are small, consequently, the results presented are preliminary. Therefore, future studies are strongly urged to acquire larger sample sizes to add to the findings of the current study.

In terms of improving on the methodology of the current study, future studies should consider; firstly, altering behavioural sampling from point-sampling to continuous sampling which may allow for more information to be obtained when observing whale behaviour. Secondly, an investigation on prey abundance, density and behaviour should be made in conjunction with using biologging tags, as this is a more robust approach in detangling the relationship between energy requirements during foraging, and the potential benefit that comes from foraging (Croll *et al.* 1998, 2005; Goldbogen *et al.* 2013b). Finally, prey availability remained similar between the two collection periods in this study (2003 – 2007 and 2022 – 2023), however, there seemed to be changes in the distribution of dense prey patches within the water column. As right whales investigated in 2022 – 2023 displayed feeding behaviour at depth, instead of the classically observed surface filtering displayed in the period 2003 – 2007, as well as in the Antarctic Peninsula and South Georgia (Hamner *et al.* 1988; Calderan *et al.* 2023), further investigation is needed to uncover whether the changes in feeding behaviour observed is a consequence of the changes in prey density or location, or if it is just an anomaly witnessed during the collection periods of this study.

CHAPTER 5 REFERENCES

Acevedo-Gutiérrez A, Croll DA, Tershy BR. 2002. High feeding costs limit dive time in the largest whales. *The Journal of experimental biology* 205: 1747–1753.

Allen G. 1916. The whalebone whales of New England. *Memoirs of the Boston Society of Natural History* 8: 1–276.

Aoki K, Amano M, Mori K, Kourogi A, Kubodera T, Miyazaki N. 2012. Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. *Marine Ecology Progress Series* 444: 289–301.

Armstrong D, Verheye H, Kemp A. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Fecundity estimates of the dominant copepod, *Calanoides carinatus*. *Progress in Oceanography* 28: 167–188.

Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100–103.

Baker C, Patenaude N, Bannister J, Robins J, Kato H. 1999. Distribution and diversity of mtDNA lineages among southern right whales (*Eubalaena australis*) from Australia and New Zealand. *Marine Biology* 134: 1–8.

Bannister J. 2009. Southern right whale aerial survey, southern Australian coast, 2009. Final report on work funded by the Island Foundation. Massachusetts (MA).: pp 17.

Bannister J. 2018. Monitoring population dynamics of ‘western’ right whales off southern Australia 2015−2018. Final report on activities for 2017. *Final report to National Environment Science Program, Australian Commonwealth Government*.

Bannister J, Hedley S, Bravington M, Burnell S. 2011. Monitoring population dynamics of right whales off southern Australia. Project 2009/41. *Final Report to The Australian Marine Mammal Centre*: 23.

Barendse J, Best PB. 2014. Shore-based observations of seasonality , movements , and group behavior of southern right whales in a nonnursery area on the South African west coast. *Marine Ecology Progress Series* 30: 1358–1382.

Bastida R, Rodríguez D. 2003. *Mamíferos marinos de Patagonia y Antártida*. Buenos Aires, Argentina: Vazquez Mazzini. pp 208.

Bastida R, Rodríguez D. 2009. *Mamíferos Marinos de Patagonia y Antártida*. Buenos Aires: Vázquez Manzini.

Baumgartner M, Lysiak N, Esch H, Zerbini A, Berchok C, Clapham P. 2013. Associations between North Pacific right whales and their zooplanktonic prey in the southeastern Bering Sea. *Marine Ecololgy Progress Series* 490: 267–285.

Baumgartner M, Cole T, Campbell R, Teegarden G, Durbin E. 2003. Associations between North Atlantic right whales and their prey, *Calanus finmarchicus*, over diel and tidal time scales. *Marine Ecology Progress Series* 264: 155–166.

Baumgartner M, Mate B. 2003. Summertime foraging ecology of North Atlantic right whales. *Marine Ecology Progress Series* 264: 123–135.

Baumgartner MF, Lysiak NSJ, Schuman C, Urban-Rich J, Wenzel FW. 2011. Diel vertical migration behavior of *Calanus finmarchicus* and its influence on right and sei whale occurrence. *Marine Ecology Progress Series* 423: 167–184.

Baumgartner MF, Mayo CA, Kenney RD. 2007. Enormous carnivores, microscopic food, and a restaurant that's hard to find. Pp. 138–171 *The urban whale: North Atlantic right whales at the crossroads.* Cambridge, MA: Harvard University Press.

Baumgartner MF, Wenzel FW, Lysiak NSJ, Patrician MR. 2017. North Atlantic right whale foraging ecology and its role in human-caused mortality. *Marine Ecology Progress Series* 581: 165–181.

Van den Berg GL, Vermeulen E, Valenzuela LO, Bérubé M, Ganswindt A, Gröcke DR, Hall G, Hulva P, Neveceralova P, Palsbøll PJ, Carroll EL. 2021. Decadal shift in foraging strategy of a migratory southern ocean predator. *Global Change Biology* 27: 1052–1067.

Berta A, Sumich JL, Kovacs KM. 2005. *Marine mammals: evolutionary biology*. Academic Press.

Best PB, Bannister J, Brownell Jr R, Donovan G. 2001a. Right whales: worldwide status. *Journal of Cetacean Research & Management*: 1–60.

Best PB, Ross G. 1896. Catches of right whales from shore-based establishments in southern Africa, 1792–1975. *Report of the International Whaling Commission (Special Issue 10)*: 275–289.

Best PB. 1987. Estimates of landed catch of right (and other whalebone) whales in the American fishery, 1805–1909. *Fishery Bulletin*, 403–418.

Best PB. 1994. Seasonality of reproduction and the length of gestation in southern right whales *Eubalaena australis*. *Journal of Zoology* 232: 175–189.

Best PB, Glass J, Ryan P, Dalebout M. 2009. Cetacean records from Tristan de Cunha, South Atlantic. *Journal of Marine Biological Association U K* 89: 1023–1032.

Best PB, Payne R, Rowntree V, Palazzo J, Both M. 1993. Long-range movements of South Atlantic right whales, *Eubalaena australis*. *Marine Mammal Science* 9: 227–234.

Best PB. 1970. Exploitation and recovery of right whales *Eubalaena australis* off the Cape Province. *Investigational Report, Division of Sea Fisheries, Republic of South Africa* 80: 1–20.

Best PB. 1990. Trends in the inshore right whale population off South Africa, 1969–1987. *Marine Mammal Science* 6: 93–108.

Best PB. 1993. Increase rates in severely depleted stocks of baleen whales. *ICES Journal of marine Science*

50: 169–186.

Best PB. 2000. Coastal distribution, movements and site fidelity of right whales *Eubalaena australis* off South Africa, 1969–1998. *South African Journal of Marine Science* 22: 43–55.

Best PB. 2006. The presence of right whales in summer on the west coast of South Africa: the evidence from historical records. *African Journal of Marine Science* 28: 159–166.

Best PB. 2007. *Whales and dolphins of the southern African subregion*. Cambridge University Press.

Best PB, Brandão A, Butterworth DS. 2001b. Demographic parameters of southern right whales off South Africa. *Journal of Cetacean Research and Management*: 161–169.

Best PB, Mate B. 2023. Sighting history and observations of southern right whales following satellite tagging off South Africa. *J. Cetacean Res. Manage.* 9: 111–114.

Best PB, Schell D. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Marine Biology* 124: 483–494.

Bode-Dalby M, Würth R, De Oliveira LDF, Lamont T, Verheye HM, Schukat A, Hagen W, Auel H. 2023. Small is beautiful: The important role of small copepods in carbon budgets of the southern Benguela upwelling system. *Journal of Plankton Research* 45: 110–128.

Bollens S, Frost B. 1989. Predator-induced diet vertical migration in a planktonic copepod. *Journal of Plankton Research* 11: 1047–1065.

Booth A. 1964. American Whalers in South African Waters. *South African Journal of Economics* 32: 278–282.

Borchers P, Hutchings L. 1986. Starvation tolerance, development time and egg production of *Calanoides carinatus* in the Southern Benguela Current. *Journal of Plankton Research* 8: 855–874.

Brandão A, Ross-Gillespie A, Vermeulen E, Butterworth DS. 2023. A photo-identification-based assessment model of southern right whales *Eubalaena australis* surveyed in South African waters, with a focus on recent low counts of mothers with calves. *African Journal of Marine Science* 45: 1–13.

Brandão A, Vermeulen E, Ross-gillespie A, Findlay K, Butterworth DS. 2018. Updated application of a photo-identification based assessment model to southern right whales in South African waters, focussing on inferences to be drawn from a series of appreciably lower counts of calving females over 2015 to 2017. *IWC Scientific Committee Report* SC/67B/SH2.

Brodie PF. 1975. Cetacean Energetics, an Overview of Intraspecific Size Variation. *Ecology* 56: 152–161.

Brownell RL, Clapham PJ, Miyashita T, Kasuya T. 2001. Conservation status of North Pacific right whales. *Journal of Cetacean Research and Management.* 2: 269–286.

Burnell S. 2001. Aspects of reproductive biology, movements and site fidelity of right whales off Australia. *Journal of Cetacean Research and Management Issue* 2: 89–102.

Butterworth DS, Best PB. 1990. Implications of the recovery rate of the South African right whale population for baleen whale population dynamics. *Report of the International Whaling Commission* 40: 433–447.

Cade DE, Barr KR, Calambokidis J, Friedlaender AS, Goldbogen JA. 2017. Determining forward speed from accelerometer jiggle in aquatic environments. *Journal of Experimental Biology* 221: jeb170449.

Calderan SV., Dornan T, Fielding S, Irvine R, Jackson JA, Leaper R, Liszka CM, Olson PA, Collins MA. 2023. Observations of southern right whales (*Eubalaena australis*) surface feeding on krill in austral winter at South Georgia. *Marine Mammal Science*: 1–7.

Carroll E, Baker C, Watson M, Alderman R, Bannister J, Gaggiotti O, Gröcke D, Patenaude N, Harcourt R. 2015. Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. *Scientific Reports* 5: 16182.

Carroll E, Childerhouse S, Fewster R, Patenaude N, Steel D, Dunshea G, Boren L, Baker C. 2013. Accounting for female reproductive cycles in a superpopulation capture–recapture framework. *Ecological Applications* 23: 1677–1690.

Carroll E, Patenaude N, Alexander A, Steel D, Harcourt R, Childerhouse S, Smith S, Bannister J, Constantine R, Baker C. 2011a. Population structure and individual movement of southern right whales around New Zealand and Australia. *Marine Ecology Progress Series* 432: 257–268.

Carroll E, Patenaude N, Childerhouse S, Kraus S, Fewster R, Baker C. 2011b. Abundance of the New Zealand sub-Antarctic southern right whale population estimated from photo_identification and genotype mark-recapture. *Marine Biology* 158: 2565–2575.

Carroll E, Rayment W, Alexander A, Baker C, Patenaude N, Steel D, Constantine R, Cole R, Boren L, Childerhouse S. 2014. Reestablishment of former wintering grounds by New Zealand southern right whales. *Marine Mammal Science* 30: 206–220.

Carroll E, Alderman R, Bannister JL, Bérubé M, Best PB, Boren L, Baker CS, Constantine R, Findlay K, Harcourt R, Lemaire L, Palsbøll PJ, Patenaude NJ, Rowntree VJ, Seger J, Steel D, Valenzuela LO, Watson M, Gaggiotti OE. 2019. Incorporating non-equilibrium dynamics into demographic history inferences of a migratory marine species. *Journal of Heredity* 122: 53–68.

Carroll E, Ott PH, McMillan LF, Vernazzani BG, Neveceralova P, Vermeulen E, Gaggiotti OE, Andriolo A, Scott Baker C, Bamford C, Best P, Cabrera E, Calderan S, Chirife A, Fewster RM, Flores PAC, Frasier T, Freitas TRO, Groch K, Hulva P, Kennedy A, Leaper R, Leslie MS, Moore M, Oliveira L, Seger J, Stepien EN, Valenzuela LO, Zerbini A, Jackson JA. 2020. Genetic diversity and connectivity of southern right whales (*Eubalaena australis*) found in the Brazil and Chile-Peru wintering grounds and the South Georgia (Islas Georgias del Sur) feeding ground. *Journal of Heredity* 111: 263–276.

Charlton C, Ward R, McCauley RD, Brownell RL, Guggenheimer S, Salgado Kent CP, Bannister JL. 2019. Southern right whales (*Eubalaena australis*) return to a former wintering calving ground: Fowlers Bay, South Australia. *Marine Mammal Science* 35: 1–25.

Charlton CM. 2017. Population demographics of southern right whales (*Eubalaena australis*) in Southern Australia. PhD dissertation, Curtin University, Bently, Western Australia.

Chavez F, Messié M. 2009. A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*. 83: 80–96.

Childerhouse S, Carroll E, Rayment W. 2009. Preliminary trip report for southern right whale research trip to the Auckland Islands July/August 2009. Report to the New Zealand Department of Conservation. Wellington, New Zealand.: pp 4.

Christiansen F, Vivier F, Charlton C, Ward R, Amerson A, Burnell S, Bejder L, Burnell AAS, Bejder L. 2018. Maternal body size and condition determine calf growth rates in southern right whales. *Marine Ecology Progress Series* 592: 267–282.

Clapham P. 2001. Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science* 17: 432–436.

Clapham PJ, Good C, Quinn SE, Reeves RR. 2004. Distribution of North Pacific right whales (*Eubalaena japonica*) as shown by 19th and 20th century whaling catch and sighting records. *Journal of Cetacean Research and Management* 6: 1–6.

Cooke J, Rowntree V, Payne R. 2001. Estimates of demographic parameters for southern right whales (*Eubalaena australis*) observed off Península Valdés, Argentina. *Journal of Cetacean Research and Management Spec Issue* 2: 125–132.

Corkeron PJ, Connor RC. 1999. Why do baleen whales migrate? *Marine Mammal Science* 15: 1228–1245.

Costa P, Piedra M, Franco P, Paez E. 2007. Distribution and habitat use patterns of southern right whales, *Eubalaena australis*, off Uruguay. *Journal of Cetacean Research and Management* 9: 45–51.

Costa P, Praderi R, Piedra M, Franco-Fraguas P. 2005. Sightings of southern right whales, Eubalaena australis, off Uruguay. *Latin American Journal of Aquatic Mammals* 4: 157–61.

Croll D, Marinovic B, Benson S, Chavez F, Black N, Ternullo R, Tershy B. 2005. From wind to whales: Trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289: 117–130.

Croll D, Tershy B, Hewitt R, Demer D, Fiedler P, Smith S, Armstrong W, Popp J, Kiekhefer T, Lopez V, Gendron D. 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep Sea Research Part II: Topical Studies in Oceanography* 45: 1353–1371.

Cummings WC. 1985. Right whales, *Eubalaena glacialis* (Muller, 1776) and *Eubalaena australis* (Desmoulins, 1822). Pp. 275–304 *Handbook of Marine Mammals*. San Diego, CA: Academic Press.

Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon, J. L. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science* 57: 603–618.

Cushing D. 1969. Upwelling and fish production. *FAO Fisheries Technical Paper* 84: 40.

D’Agostino VC, Hoffmeyer MS, Degrati M. 2016. Faecal analysis of southern right whales (*Eubalaena australis*) in Península Valdés calving ground, Argentina: *Calanus australis*, a key prey species. *Journal of the Marine Biological Association of the United Kingdom* 96: 859–868.

Davidson A, Rayment W, Slooten E. 2016. Population dynamics of New Zealand southern right whale (*Eubalaena australis*). *International Whaling Commission document SC/67A/SH/08*.

Dawbin W. 1986. Right whales caught in waters around south eastern Australia and New Zealand during the nineteenth and early twentieth centuries. *Report of the International Whaling Commission Special Issue* 10: 261–267.

Demarcq H, Barlow R, Shillington F. 2003. Climatology and variability of sea surface temperature and surface chlorophyll in the Benguela and Agulhas Bank ecosystems as observed by satellite imagery. *African Journal of Marine Science* 25: 353–372.

Dey SP, Vichi M, Fearon G, Seyboth E, Findlay KP, Meynecke JO, De Bie J, Lee SB, Samanta S, Barraqueta JM, Roychoudhury AN, Mackey B. 2021. Oceanographic anomalies coinciding with humpback whale super-group occurrences in the Southern Benguela. *Scientific Reports* 11: 1–13. Nature Publishing Group UK.

Diedrich CG. 2013. Evolution of white and megatooth sharks, and evidence for early predation on seals, sirenians, and whales. *Natural Science* 5: 1203–1218.

Domenici P. 2001. The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comparative biochemistry and physiology A* 131: 169–182.

Van Duren L, Videler J. 1996. The trade-off between feeding, mate seeking and predator avoidance in copepods: behavioural responses to chemical cues. *Journal of Plankton Research* 18: 805–818.

Elwen SH, Best PB. 2004a. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa II: Within bay distribution. *Marine Mammal Science* 20: 583–601.

Elwen SH, Best PB. 2004b. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa I: Broad scale patterns. *Marine Mammal Science* 20: 567–582.

Eschricht D, Reinhardt J. 1866. On the Greenland right whale (*Balaena mysticetus* Linn.) with especial reference to its geographical distribution and migrations in times past and present, and to its external and internal characteristics. Pp. 1–150 *Recent Memoirs on the Cetacea by Professors Eschricht, Reinhardt, and Lilljeborg*. London: Ray Society.

Espírito Santo S, Franco D, Groch K. 2009. Geostatistical density analysis of southern right whale (*Eubalaena australis*) occurrences along the coast of Santa Catarina, Southern Brazil - preliminary information. Paper SC/61/BRG15 presented to the IWC Scientific Committee, June 2009, Madeira, Portug: 5.

Failla M, Vermeulen E, Carabajal M, Arruda J, Godoy H, Lapa A, Mora G, Urrutia C, Balbiano A, Cammareri A. 2008. Historical records of southern right whales (*Eubalaena australis*) of the province Rio Negro, North Patagonia, Argentina (1991-2008). Paper SC/60/BRG1 presented to the IWC Scientific Committee, June 2008, Santiago, Chile.

Falk-Petersen S, Leu E, Berge J, Kwasniewski S, Nygård H, Røstad A, Keskinen E, Thormar J, Von Quillfeldt C, Wold A, Gulliksen B. 2008. Vertical migration in high Arctic waters during autumn 2004. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 2275–2284.

Findlay KP, Seakamela SM, Meÿer MA, Kirkman SP, Barendse J, Cade DE, Hurwitz D, Kennedy AS, Kotze PGH, McCue SA, Thornton M, Vargas-Fonseca OA, Wilke CG. 2017. Humpback whale 'super-groups' - A novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) in the Benguela Upwelling System. *PLoS ONE* 12: e0172002.

Fortune SME, Ferguson SH, Trites AW, Hudson JM, Baumgartner MF. 2020. Bowhead whales use two foraging strategies in response to fine-scale differences in zooplankton vertical distribution. *Scientific Reports* 10: 1–18.

Friedlaender A, Halpin P, Qian S, Lawson G, Wiebe P, Thiele D, Read A. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series* 317: 297–310.

Friedlaender AS, Hazen EL, Goldbogen JA, Stimpert AK, Calambokidis J, Southall BL. 2016. Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological applications: a publication of the Ecological Society of America* 26: 1075–1085.

Fudge D, Szewciw L, Schwalb A. 2009. Morphology and development of blue whale baleen: an annotated translation of Tycho Tullberg's classic 1883 paper. *Aquatic Mammals* 35: 226–252.

Galletti Vernazzani B, Cabrera E, Brownell R. 2014. Eastern South Pacifc southern right whale photo-identifcation catalog reveals behavior and habitat use patterns. *Marine Mammal Science* 30: 389–398.

Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE, Norman B, Hays GC, Quintana F, Grundy E, Campagna C, Trites AW, Block BA, Wilson RP. 2011. Convergent evolution in locomotory patterns of flying and swimming animals. *Nature Communications* 2: 352.

Goldbogen JA, Cade DE, Boersma AT, Calambokidis J, Kahane-Rapport SR, Segre PS, Stimpert AK, Friedlaender AS. 2017a. Using digital tags with integrated video and inertial sensors to study moving morphology and associated function in large aquatic vertebrates. *Anatomical Record* 300: 1935–1941.

Goldbogen JA, Cade DE, Calambokidis J, Friedlaender AS, Potvin J, Segre PS, Werth AJ. 2017b. How baleen whales feed: the biomechanics of engulfment and filtration. *Annual Review of Marine Science* 9: 367–386.

Goldbogen JA, Calambokidis J, Croll DA, McKenna MF, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE, Tershy BR. 2012. Scaling of lunge-feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Functional Ecology* 26: 216–226.

Goldbogen JA, Calambokidis J, Friedlaender AS, Francis J, DeRuiter SL, Stimpert AK, Falcone E, Southall BL. 2013a. Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge-feeding blue whales. *Biology letters* 9: 20120986.

Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *Journal of Experimental Biology* 214: 698–699.

Goldbogen JA, Friedlaender AS, Calambokidis J, McKenna MF, Simon M, Nowacek DP. 2013b. Integrative approaches to the study of baleen whale diving behavior, feeding performance, and foraging ecology. *BioScience* 63: 90–100.

González Carman V, Piola A, O'Brien TD, Tormosov DD, Acha EM. 2019. Circumpolar frontal systems as potential feeding grounds of Southern Right whales. *Progress in Oceanography* 176: 102123.

Greene CH, Pershing AJ. 2004. Climate and the conservation biology of North Atlantic right whales: The right whale at the wrong time? *Frontiers in Ecology and the Environment* 2: 29–34.

Greene CH, Pershing AJ, Kenney RD, Jossi JW. 2003. Impact of climate variability on the recovery of endangered North Atlantic right whales. *Oceanography* 16: 98–103.

Groch K., Fabián M., Palazzo JT. 2003. Monitoring behavioral responses of southern right whales to whale watching activities in the southern Brazilian coast and an evaluation of its conservation implications. Paper SC/55/WW5 presented to the IWC Scientific Committee, May 2003, Berlin. [Paper a: 23.

Groch K, Palazzo J, Flores P, Ardler F, Fabian M. 2005. Recent rapid increase in the right whale (*Eubalaena australis*) population off southern Brazil. *Latin American Journal of Aquatic Mammals* 4: 41–47.

Hamner WM, Stone GS, Obst BS. 1988. Behavior of southern right whales, *Eubalaena australis*, feeding on the Antarctic krill, *Euphausia superba*. *Fishery Bulletin* 86: 143–150.

Harcourt R, Van der Hoop J, Kraus S, Carroll E. 2019. Future directions in *Eubalaena* spp.: comparative research to inform conservation. *Frontiers in Marine Science* 5: 530.

Hardman-Mountford NJ, Richardson AJ, Agenbag JJ, Hagen E, Nykjaer L, Shillington FA, Villacastin C. 2003. Ocean climate of the South East Atlantic observed from satellite data and wind models. *Progress in Oceanography* 59: 181–221.

Hays G. 1995. Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. *Limnology and Oceanography* 40: 1461–1465.

Hazen EL, Friedlaender AS, Goldbogen JA. 2015. Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science advances* 1: e1500469.

Heileman S, O'Toole MJ. 2008. Benguela current LME. *The UNEP Large Marine Ecosystem Report: A perspective of changing conditions in LMEs of the world's regional seas UNEP Regional Seas Report and Studies*: 100–142.

Hill A, Hickey BM, Shillington FA, Strub PT, Brink KH, Barton ED, Thomas A. 1998. Eastern Ocean Boundaries. Pp. 29–86 *The Global Coastal Ocean Regional Studies and Syntheses, The Sea, Volume 11*. New York: J. Wiley and Sons.

Hlista BL, Sosik HM, Traykovski LVM, Kenney RD, Moore MJ. 2009. Seasonal and interannual correlations between right-whale distribution and calving success and chlorophyll concentrations in the Gulf of Maine, USA. *Marine Ecology Progress Series* 394: 289–302.

Hoffmeyer M, Lindner M, Carribero A, Fulco V, Menéndez M, Fernández Severini M, Diodato S, Berasategui A, Biancalana F, Berrier E. 2010. Planktonic food and foraging of *Eubalaena australis*, on Peninsula Valdés (Argentina) nursery ground. *Revista de Biologia Marina y Oceanografia* 45: 131–139.

Van der Hoop JM, Nousek-McGregor AE, Nowacek DP, Parks SE, Tyack P, Madsen PT. 2019. Foraging rates of ram-filtering North Atlantic right whales. *Functional Ecology* 33: 1290–1306.

Van der Hoop JM, Nowacek D, Moore MJ, Triantafyllou MS. 2017. Swimming kinematics and efficiency of entangled North Atlantic right whales. *Endangered Species Research* 32: 1–17.

Huggett J. 2001. Reproductive response of the copepods *Calanoides carinatus* and *Calanus agulhensis* to varying periods of starvation in the southern Benguela upwelling region. *Journal of Plankton Research* 23: 1061–1071.

Huggett J, Verheye H, Escribano R, Fairweather T. 2009. Copepod biomass, size composition and production in the Southern Benguela: Spatio-temporal patterns of variation, and comparison with other eastern boundary upwelling systems. *Progress in Oceanography* 83: 197–207.

Huntley M, Brooks E. 1982. Efects of age and food availability on diel vertical migration of *Calanus* *pacifcus*. *Marine Biology* 71: 23–31.

Hutchings L, Van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, Van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS. 2009. The Benguela Current: An ecosystem of four components. *Progress in Oceanography* 83: 15–32.

IPCC. 2014. Climate change 2014: synthesis report. P. *Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change*. Geneva, Switzerland: IPCC Geneva, Switzerland. pp 151.

Itoh K. 1970. A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts. *Bulletin of Plankton Society of Japan* 17: 1010.

IWC. 2001. Report of the Workshop on the Comprehensive Assessment of Right Whales: A Worldwide Comparison. *Journal of Cetacean Research and Management Special Issue*: 1–60.

IWC. 2013. Report of the IWC workshop on the assessment of southern right whales. *Journal of Cetacean Research and Management*: 450–451.

Jackson J, Stowasser G, Carroll E, Christiansen F, Baker C, Bassoi M, Buss D, Calderan S, Cheeseman T, Collins M, Ensor P, Groch K, Hall A, Kershaw J, Leaper R, Macdonald D, Moore M, Olson P, Passadore C, Riet-Sapriza F, Costa-Urrutia P, Beretta N, Rowntree V, Sironi M, Trathan P, Uhart M, Valenzuela L, Vermeulen E, Vilches F, Zerbini A, Kennedy A. 2021. Southern right whale population connections, trophic ecology and health on their South Georgia (Islas Georgias del Sur, SG/GS) feeding ground. P. *SC/68c/CMP/08 Rev1 Presented to Sci. Int. Whal. Comm* 1–17.

Jackson JA, Patenaude NJ, Carroll EL, Scott Baker C. 2008. How few whales were there a er whaling ? Inference from contemporary mtDNA diversity Related papers. *Molecular Ecology* 17: 236–251.

Jarre A, Hutchings L, Kirkman SP, Kreiner A, Tchipalanga PCM, Kainge P, Uanivi U, Van der Plas AK, Blamey LK, Coetzee JC, Lamont T, Samaai T, Verheye HM, Yemane DG, Axelsen BE, Ostrowski M, Stenevik EK, Loeng H. 2015. Synthesis: Climate effects on biodiversity, abundance and distribution of marine organisms in the Benguela. *Fisheries Oceanography* 24: 122–149.

Johnson MP, Tyack PL. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28: 3–12.

Jönsson KI. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78: 57–66.

Kawaguchi S, Kurihara H, King R, Hale L, Berli T, Robinson JP, Ishimatsu A. 2011. Will krill fare well under Southern Ocean acidification? *Biology Letters* 7: 288–291.

Keith S, Bull J. 2017. Animal culture impacts species' capacity to realise climate-driven range shifts.

Ecography 40: 296–304.

Kenney R. 2002. *Eubalaena glacialis*, *E. japonica*, and *E. australis*. *Encyclopedia of Marine Mammals*. Academic Press.

Kenney RD, Hyman MAM, Owen RE, Scott GP, Winn HE. 1986. Estimation of prey densities required by western North Atlantic right whales. *Marine Mammal Science* 2: 1–13.

Kenney RD, Mayo CA, Winn HE. 2020. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: a review of hypotheses. *Journal of Cetacean Research and Management Special Issue* 251–260.

Kiørboe T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in Marine Biology* 29: 1–72.

Kirkman SP, Holness S, Harris LR, Sink KJ, Lombard AT, Kainge P, Majiedt P, Nsiangango SE, Nsingi KK, Samaai T. 2019. Using Systematic Conservation Planning to support Marine Spatial Planning and achieve marine protection targets in the transboundary Benguela Ecosystem. *Ocean and Coastal Management* 168: 117–129.

Klevjer TA, Tarling GA, Fielding S. 2010. Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea. *Marine Ecology Progress Series* 409: 157–170.

Knowlton A, Kraus S, Kenney R. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). *Canadian Journal of Zoology* 72: 1297–1305.

Kraus S, Pace R, Frasier T. 2007. High investment, low return: the strange case of reproduction in *Eubalaena glacialis*. Pp. 172–199 *The urban whale: North Atlantic right whales at the crossroads*. Cambridge, MA: Harvard University Press.

Laidre K, Heide-Jørgensen M, Nielsen T. 2007. Role of the bowhead whale as a predator in West Greenland. *Marine Ecology Progress Series* 346: 285–297.

Lambertsen RH, Rasmussen KJ, Lancaster WC, Hintz RJ. 2005. Functional morphology of the mouth of the bowhead whale and its implications for conservation. *Journal of Mammalogy* 86: 342–352.

Lamont T, García-Reyes M, Bograd SJ, Van der Lingen CD, Sydeman WJ. 2018. Upwelling indices for comparative ecosystem studies: Variability in the Benguela Upwelling System. *Journal of Marine Systems* 188: 3–16.

Laws R. 1985. The ecology of the southern ocean. *American Scientist* 73: 26–40.

Leandro L, Rolland R, Roth P, Lundholm N, Wang Z, Doucette GJ. 2010. Exposure of the North Atlantic right whale *Eubalaena glacialis* to the marine algal biotoxin, domoic acid. *Marine Ecolology Progress Series* 398: 287–303.

Leaper R, Cooke J, Trathan P, Reid K, Rowntree V, Payne R. 2006. Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biology Letters* 2: 289–292.

Lenz J. 2000. Introduction. Pp. 1–32 *ICES Zooplankton Methodology Manueal*. London: Academic Press.

Lett C, Veitch J, Van der Lingen C., Hutchings L. 2007. Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. *Marine Ecology Progress Series* 347: 247–259.

Van der Lingen CD, Hutchings L, Lamont T, Pitcher GC. 2016. Climate change, dinoflagellate blooms and sardine in the southern Benguela current large marine ecosystem. *Environmental Development* 17: 230–243.

Lockyer C. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. *Mammals in the seas* 3: 379–487.

Lockyer C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. *Report to the International Whaling Commission* 6: 27–50.

Lockyer C. 1986. Body fat condition in northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 142–147.

Lockyer C. 2007. All creatures great and smaller: A study in cetacean life history energetics. *Journal of the Marine Biological Association of the United Kingdom* 87: 1035–1045.

Lodi L, Tardelli Rodrigues T. 2007. Southern right whale on the coast of Rio de Janeiro State, Brazil: conflict between conservation and human activity. *Journal of Marine Biological Association U K* 87: 105–107.

Loeb V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387: 897–900.

Lusseau D. 2003. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology* 17: 1785–1793.

Lutjeharms JRE, Stockton PL. 1987. Kinematics of the upwelling front off Southern Africa. *South African Journal of Marine Science* 5: 35–49.

Mate BR, Best PB, Lagerquist BA, Winsor MH. 2011. Coastal, offshore, and migratory movements of South African right whales revealed by satellite telemetry. *Marine Mammal Science* 27: 455–476.

Matthews LH. 1932. Lobster-krill, anomuran crustacea that are the food of whales. *Discovery Reports* 5: 467–484.

Mauchline J. 1998. The biology of calanoid copepods. *Advance in Marine Biology 33*. Academic Press.

Mayo CA, Letcher BH, Scott S. 2001. Zooplankton filtering efficiency of the baleen of a North Atlantic right whale, *Eubalaena glacialis*. *Journal of Cetacean Research and Management (Special Issue)*: 225–229.

Mayo CA, Marx M. 1990. Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Canadian Journal of Zoology* 68: 2214–2220.

Menéndez M, Berasategui A, Lindner M, Diodato S, Fernández-Severini M, Hoffmeyer M. 2007. Trophic spectrum of southern right whale *Eubalaena australis* by means of faecal analysis. *Biocell* 31: 347.

Messié M, Ledesma J, Kolber D, Michisaki R, Foley D, Chavez F. 2009. Potential new production estimates in four eastern boundary upwelling ecosystems. *Progress in Oceanography* 83: 151–158.

Michaud J, Taggart CT. 2007. Lipid and gross energy content of North Atlantic right whale food, *Calanus finmarchicus*, in the Bay of Fundy. *Endangered Species Research* 3: 77–94.

Michaud J, Taggart CT. 2011. Spatial variation in right whale food, Calanus finmarchicus, in the Bay of Fundy. *Endangered Species Research* 15: 179–194.

Miller CA, Reeb D, Best PB, Knowlton AR, Brown MW, Moore MJ. 2011. Blubber thickness in right whales *Eubalaena glacialis* and *Eubalaena australis* related with reproduction, life history status and prey abundance. *Marine Ecology Progress Series* 438: 267–283.

Moore M, Berrow S, Jensen B, Carr P, Sears R, Rowntree V, Payne R, Hamilton P. 1999. Relative abundance of large whales around South Georgia (1979−1998). *Marine Mammal Science* 15: 1287–1302.

Moore S, Waite J, Friday N, Honkalehto T. 2002. Cetacean distribution and relative abundance on the centraleastern and the southeasten Bering Sea shelf with reference to oceanographic domains. *Progress in Oceanography* 55: 249–61.

Murphy EJ, Trathan PN, Watkins JL, Reid K, Meredith M, Forcada J, Thorpe SE, Johnston N, Rothery P. 2007. Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society B* 274: 3057–3067.

Nicol S, Worby A, Leaper R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Marine and Freshwater Research* 59: 361–382.

Nousek-McGregor A. 2010. The cost of locomotion in North Atlantic right whales *Eubalaena glacialis*. Duke University, Durham, NC.

Nowacek DP, Johnson MP, Tyack PL, Shorter KA, McLellan WA, Pabst DA. 2001. Buoyant balaenids: The ups and downs of buoyancy in right whales. *Proceedings of the Royal Society B: Biological Sciences* 268: 1811–1816.

Oftedal OT. 1997. Lactation in whales and dolphins: evidence of divergence between baleen-and toothed-species. *Journal of mammary gland biology and neoplasia* 2: 205–230.

Owens NJP, Hosie GW, Batten SD, Edwards M, Johns DG, Beaugrand G. 2013. All plankton sampling systems underestimate abundance: Response to "Continuous plankton recorder underestimates zooplankton abundance" by J.W. Dippner and M. Krause. *Journal of Marine Systems* 128: 240–242.

Parks SE, Warren JD, Stamieszkin K, Mayo CA, Wiley D. 2012. Dangerous dining: Surface foraging of North Atlantic right whales increases risk of vessel collisions. *Biology Letters* 8: 57–60.

Du Pasquier T. 1986. Catch history of French right whaling mainly in the South Atlantic. *Report to the International Whaling Commission Special Issue* 10: 269–274.

Patenaude N. 2003. Sightings of southern right whales around mainland New Zealand. *Science for Conservation 225*: 43–50.

Patenaude N, Baker C. 2001. Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands ofNew Zealand. *Journal of Cetacean Research and Management Special Issue* 2: 111–116.

Patenaude N, Baker C, Gales N. 1998. Observations of southern right whales on New Zealand's subantarctic wintering grounds. *Marine Mammal Science* 14: 350–355.

Patenaude N, Portway VA, Schaeff CM, Bannister JL, Best PB, Payne RS, Rowntree VJ, Rivarola M, Baker CS. 2007. Mitochondrial DNA diversity and population structure among southern right whales (*Eubalaena australis*). *Journal of Heredity* 98: 147–157.

Pauly D, Christensen V. 1995. Primary production required to sustain global fisheries. *Nature* 374: 255–257.

Payne R. 1976. At home with right whales. *National Geographic*: 322–339.

Payne R. 1986. Long term behavioral studies of the southern right whale (*Eubalaena australis*). *Report to the International Whaling Commision Special Issue* 10: 161–167.

Payne R. 1995. *Among whales*. Scribner.

Payne R, Brazier O, Dorsey EO, Perkins JS, Rowntree VJ, Titus A. 1983. External features in southern right whales (*Eubalaena australis*) and their use in identifying individuals. *Communication and Behavior of Whales*: 371–445.

Payne R, Rowntree V, Perkins J., Cooke J., Lankester K. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Península Valdés, Argentina. *Report to the International Whaling Commission Special Issue*: 271–278.

Peterson W. 1998. Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* 15: 313–326.

Peterson W, Painting S. 1990. Developmental rates of copepods *Calanus australis* and *Calanoides carinatus* in the laboratory, with discussion of methods used for calculation of development time. *Journal of Plankton Research* 12: 283–290.

Pivorunas A. 1979. Feeding mechanisms of baleen whales. *American Scientist* 67: 432–440.

Pomerleau C, Patterson T, Luque S, Lesage V, Ferguson S. 2011. Bowhead whale *Balaena mysticetus* diving and movement patterns in the eastern Canadian Arctic: Implications for foraging ecology. *Endangered Species Research* 15: 167–177.

Potvin J, Werth AJ. 2017. Oral cavity hydrodynamics and drag production in Balaenid whale suspension feeding. *PLoS ONE* 12: 1–37.

Pyenson ND, Goldbogen JA, Vogl AW, Szathmary G, Drake RL, Shadwick RE. 2012. Discovery of a sensory organ that coordinates lunge feeding in rorqual whales. *Nature* 485: 498–501.

Rayment W, Davidson A, Dawson S, Slooten E, Webster T. 2012. Distribution of southern right whales on the Auckland Islands calving grounds. *New Zealand Journal of Marine and Freshwater Research* 46: 431–436.

Reeves R, Rolland R, Clapham P. 2001. Causes of reproductive failure in North Atlantic right whales: new avenues of research. *Northeast Fisheries Science Center Report of a Workshop Held 26-28 April 2000, Falmouth, Massachusetts*: 2–17.

Reilly S, Hedley S, Borberg J, Hewitt R, Thiele D, Watkins J, Naganobu M. 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography* 51: 1397–1409.

Rendell L, Whitehead H. 2001. Culture in whales and dolphins. *Behavioral and Brain Sciences* 24: 309–382.

Richards R. 2002. Southern right whales: a reassessment oftheir former distribution and migration routes in New Zealand waters, including on the Kermadec grounds. *Journal of the Royal Society of New Zealand* 32: 355–377.

Richards R. 2009. Past and present distributions of southern right whales (*Eubalaena australis*). *New Zealand Journal of Zoology* 36: 447–459.

Richards R, Du Pasquier T. 1989. Bay whaling off Southern Africa, c. 1785–1805. *South African Journal of Marine Science* 8: 231–250.

Rolland RM, Hamilton PK, Kraus SD, Davenport B, Gillett RM, Wasser SK. 2006. Faecal sampling using detection dogs to study reproduction and health in North Atlantic right whales (*Eubalaena glacialis*). *Journal of Cetacean Research and Management* 8: 121–125.

Rouault M, Pohl B, Penven P. 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science* 32: 237–246.

Roux J, Braby R, Best P. 2015. Does disappearance mean extirpation? The case of right whales off Namibia. *Marine Mammal Science* 31: 1132–1152.

Rowntree V, Payne R, Schell D. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. *Journal of Cetacean Research and Management Special Issue* 2: 133–143.

Rowntree V, Valenzuela L, Franco-Fraguas P, Seger J. 2008. Foraging behaviour of southern right whales (*Eubalaena australis*) inferred from variation of carbon stable isotope ratios in their baleen. *Journal of Cetacean Research and Management* 2: 1–10.

Roy C, Weeks S, Rouault M, Nelson G, Barlow R, Van der Lingen C. 2001. Extreme oceanographic events recorded in the Southern Benguela during the 1999-2000 summer season. *South African Journal of Science* 97: 465–471.

Rykaczewski R, Checkley JDM. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of National Acadademic Sciences U. S. A.* 105: 1965–1970.

Ryther J. 1969. Photosynthesis and fish production in the sea. *Science* 166: 72–76.

Santos M, Siciliano S, Castro Vincente A., Alvarenga F, Zampirolli E, Pacheco de Souza S, Maranho A. 2010. Cetacean records along Sao Paulo state coast, southeastern Brazil. *Brazilian Journal of Oceanography* 58: 123–42.

Schaeff C, Best P, Rowntree V, Payne R, Jarvis C, Portway V. 1999. Dorsal skin color patterns among southern right whales (*Eubalaena australis*): genetic basis and evolutionary significance. *Journal of Heredity* 90: 464–471.

Schlaepfer M, Runge M, Sherman P. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17: 474–480.

Segre PS, Cade DE, Fish FE, Potvin J, Allen AN, Calambokidis J, Friedlaender AS, Goldbogen JA. 2016. Hydrodynamic properties of fin whale flippers predict maximum rolling performance. *The Journal of experimental biology* 219: 3315–3320.

Seyboth E, Groch KR, Dalla Rosa L, Reid K, Flores PAC, Secchi ER. 2016. Southern right whale *(Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Scientific Reports* 6: 1–8.

Shannon L V, Nelson G. 1996. The Benguela: large scale features and processes and system variability. Pp. 163–210 *The South Atlantic Past and Present Circulation*. Berlin, Heidelberg: Springer Verlag.

Shannon LV. 1985. The Benguela ecosystem Part 1. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology Annual Review*: 105–182.

Shannon LV, O'Toole MJ. 2003. Sustainability of the Benguela: ex Africa semper aliquid novi. Pp. 227–253 *Large Marine Ecosystems of the World – Trends in Exploitation, Protection and Research*. Elsevier.

Shillington FA. 1998. The Benguela upwelling system off southwestern Africa. Pp. 583–604 *The Sea*.

Wiley.

Simon M, Johnson M, Madsen PT. 2012. Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *The Journal of experimental biology* 215: 3786–3798.

Simon M, Johnson M, Tyack P, Madsen PT. 2009. Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B* 276: 3819–3828.

Sironi M. 2004. Behavior and social development of juvenile southern right whales (*Eubalaena australis*) and interspecific interactions at Península Valdés, Argentina. University of Wisconsin, Madison, WI.

Smith J, Jones D, Travouillon K, Kelly N, Double M, Bannister J. 2019. Monitoring population dynamics of 'western' right whales off southern Australia 2018−2021. Final report on activities for 2018. *Report to the National Environmental Science Program, Marine Biodiversity Hub. Western Australian Museum (lead organisation)*.

Smith T, Reeves R, Josephson E, Lund J. 2012. Spatial and seasonal distribution of American whaling and whales in the age of sail. *PLoS ONE* 7: e34905.

Stamation K, Watson M, Moloney P, Charlton C, Bannister J. 2020. Population estimate and rate of increase of southern right whales *Eubalaena australis* in Southeastern Australia. *Endangered Species Research* 41: 373–383.

Stewart S, Todd B. 2001. A note on observations of southern right whales at Campbell Island, New Zealand. *Joural of Cetacean Research and Management Special Issue* 2: 117–120.

Stone G, Florez-Gonzalez L, Katona S. 1990. Whale migration record. *Nature* 346: 705.

Stone G, Kraus S, Prescott J, Hazard K. 1988. Significant aggregations of the endangered right whale, *Eubalaena glacialis*, on the continental shelf of Nova Scotia. *The Canadian Field-Naturalist* 102: 471–474.

Sullivan B., Miller C., Peterson W., Soeldner A. 1975. A scanning electron microscope study of the mandibular morphology of boreal copepods. *Marine Biology* 30: 178–182.

Sverdrup H. 1983. On the process of upwelling. *Journal of Marine Research* 1: 155–164.

Theal G. 1900. *Records of the Cape Colony from July 1806 to May 1909, Vol. 6.* Government of Cape Colony.

Thomas PO. 1987. Social behavior, habitat use, and interspecific interactions of southern right whale, *Eubalaena australis*, mother-calf pairs. University of California, Davis.

Thomas PO, Taber SM. 1984. Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behavior* 88: 42–60.

Thompson D, Fedak MA. 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* 61: 287–296.

Tormosov DD, Mikhaliev YA, Best PB, Zemsky VA, Sekiguchi K, Brownell RL. 1998. Soviet catches of southern right whales *Eubalaena australis*, 1951-1971. Biological data and conservation implications. *Biological Conservation* 86: 185–197.

Torres L, Smit T, Sutton P, MacDiarmid A, Bannister J, Miyashita T. 2013. From exploitation to conservation: habitat models using whaling data predict distribution patterns and threat exposure of an endangered whale. *Diversity and Distributions* 19: 1138–1152.

Townsend CH. 1935. The distribution of certain whales as shown by the logbook records of American whaleships. *Zoologica* 19: 1–50.

Trathan P, Murphy E. 2003. Sea surface temperature anomalies near South Georgia: Relationships with the Pacific El Niño regions. *Journal of Geophysics. Res.* 108: 1–10.

Trathan PN, Murphy EJ, Forcada J, Croxall JP, Reid K, Thorpe SE, Boyd IL, Wanless S, Camphuysen CJ. 2006. Pp. 28–45 *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge, UK: Cambridge University Press.

Tulloch VJD, Plagányi ÉE, Matear R, Brown CJ, Richardson AJ. 2018. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish and Fisheries* 19: 117–137.

Valenzuela LO, Rowntree VJ, Sironi M, Seger J. 2018. Stable isotopes (δ^{15}N, δ^{13}C, δ^{34}S) in skin reveal diverse food sources used by southern right whales *Eubalaena australis*. *Marine Ecology Progress Series* 603: 243–255.

Valenzuela LO, Sironi M, Rowntree VJ, Seger J. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology* 18: 782–791.

Verheye HM, Richardson A. 1998. Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951-1996): Bottom-up or top-down control? *ICES Journal of Marine Science* 55: 803–807.

Verheye HM. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Abundance, distribution and estimated production of mesozooplankton with special reference to *Calanoides carinatus* (Krøyer, 1849). *Progress in Oceanography* 28: 91–110.

Verheye HM, Hutchings L, Huggett JA, Painting SJ. 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. *South African Journal of Marine Science* 12: 561–584.

Verheye HM, Lamont T, Huggett JA, Kreiner A, Hampton I. 2016. Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME). *Environmental Development* 17: 75–92.

Verheye HM, Richardson AJ, Hutchings L, Marska G, Gianakouras D. 1998. Long-term trends in the abundance and community structure of coastal zooplankton in the southern benguela system, 1951-1996. *South African Journal of Marine Science*: 317–332.

Vermeulen E, Thavar MT, Glarou M, Ganswindt A, Christiansen F. 2023. Decadal decline in maternal body condition of a Southern Ocean capital breeder. *Scientific Reports* 13: 3228.

Vermeulen E, Wilkinson C, Thornton M. 2019. Report of the 2018 South African Southern Right Whale Aerial Surveys. *Reports of the International Whaling Commission* SC/68A/SH/: 1–25.

Walkusz W, Williams WJ, Harwood LA, Moore SE, Stewart BE, Kwasniewski S. 2012. Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (*Balaena mysticetus*) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). *Deep Sea Research Part I: Oceanographic Research Papers* 69: 25–35.

Wang D, Gouhier TC, Menge BA, Ganguly AR. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518: 390–394.

Ward EJ, Holmes EE, Balcomb KC. 2009. Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology* 46: 632–640.

Watkins WA, Schevill WE. 1976. Right whale feeding and baleen rattle. *Journal of Mammalogy* 57: 58–66.

Watkins WA, Schevill WE. 1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. *Journal of Mammalogy* 60: 155–163.

Watson M, Westhorpe I, Bannister J, Hedley S, Harcourt R. 2013. Final report on the assessment of numbers and distribution of southern right whales in Southeast Australia. *Report to the Australian Marine Mammal Centre*.

Weir C, Stanworth A. 2019. The Falkland Islands (Malvinas) as sub-Antarctic foraging, migratory and wintering habitat for southern right whales. *Journal of Marine Biological Association U K* 100: 1–11.

Werth A. 2000. Feeding in marine mammals. Pp. 475–526 *Feeding, Form, Function, and Evolution in Tetrapod Vertebrates*. Academic Press.

Werth A. 2001. How do mysticetes remove prey trapped in baleen? *Bulletin of the Museum of Comparative Zoology* 156: 189–203.

Werth AJ. 2004. Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *Journal of Experimental Biology* 207: 3569–3580.

Werth AJ, Potvin J. 2016. Baleen hydrodynamics and morphology of cross-flow filtration in balaenid whale suspension feeding. *PLoS ONE* 11: 1–21.

Whitehead H, Moore MJ. 1982. Distribution and movements of West Indian humpback whales in winter. *Canadian Journal of Zoology* 60: 2203–2211.

Whitehead H, Rendell L, Osborne RW, Würsig B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation* 120: 427–437.

Williams R, Vikingsson GA, Gislason A, Lockyer C, New L, Thomas L, Hammond PS. 2013. Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. *ICES Journal of Marine Science* 70: 1273–1280.

Williams TM. 2006. *Physiological and ecological consequences of extreme body size in whales*. University of California Press.

Williams TM, Haun J, Davis RW, Fuiman LA, Kohin S. 2001. A killer appetite: metabolic consequences of carnivory in marine mammals. *Comparative biochemistry and physiology A* 129: 785–796.

Wishner KF, Schoenherr JR, Beardsley R, Chen C. 1995. Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime right whale feeding area in the southwestern Gulf of Maine. *Continental Shelf Research* 15: 475–507.

Woodward B. 2006. Locomotory strategies, dive dynamics, and functional morphology of the mysticetes: Using morphometrics, osteology, and DTAG data to compare swim performance in four species of baleen whales. University of Maine, Orono.

Wooster W, Reid J. 1963. Eastern boundary currents. Pp. 253–280 *The sea, vol. 2*. New York: Interscience Pub.

Zerbini A, Rosenbaum H, Mendez M, Zucunza F, Andriolo A, Harris G. 2015. Tracking southern right whales through the southwest Atlantic: An update on movements , migratory routes and feeding grounds. Paper SC/66a/BRG22 presented at the 66th annual meeting of the International Whaling Commission Scientific Committee: 1–15.

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