Review of Hector's and Māui dolphin diet, nutrition and potential mechanisms of nutritional stress

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Introduction

Hector's dolphin is a small black, white and grey dolphin endemic to the waters around the North and South Island of New Zealand. Two subspecies, Hector's (*Cephalorhnchus hectori hectori*) and Māui dolphin (*Cephalorhynchus hectori Māui*) are currently classified as Nationally Endangered and Nationally Critical respectively, by the Department of Conservation New Zealand Threat Classification System (Baker et al. 2016).

An update of the risk assessment of threats to Hector's and Māui dolphins to inform a revised Threat Management Plan (TMP) for the species is currently underway. Information with respect to climate and indirect-fishing effects on Hector's and Māui dolphin populations is currently made more difficult by fundamental information (e.g. with respect to dolphin diet, nutrition and potential mechanisms of nutritional stress) being spread across several publications, including the grey literature.

In order to address this research need of the TMP risk assessment, a review of this information was undertaken in order to provide consultation documents to Treaty Partners, stakeholders, the public and risk assessment team. This review aims to summarise the information in a format that will be useful for understanding Hector's/ Māui dolphin diet and the risk factors that might impact on nutrition and population recovery.

The specific objectives of this research were to:

i. review and collate the available information on the diet of Hector's and Māui dolphin;
ii. identify possible sources of nutritional stress; and
iii. identify the key research gaps with focus on research that will be useful to inform conservation and management actions (management to reduce threats and promote population recovery and resilience)

Methods

Review of dietary information

Search terms used to find publications included "Hector's", "dolphin", "diet" and "nutrition". Faculty, as well as two past and one present student from Otago University were consulted for material and suggestions, as were contacts with expertise in given areas from NIWA, DOC and WWF.

To describe how nutritional stress might impact Hector's dolphins I inferred from our understanding of energy inputs and outputs from biologically-similar species including the physiologically similar Commerson's dolphin (*Cephalorhynchus commersonii*). I also considered the particular morphological, physiological and behavioural characteristics of Hector's dolphins to predict how nutritional stress might influence individuals, reproduction and ultimately populations. Comparative case studies of Commerson's dolphins, killer whales, sea otters and yellow-eyed penguins are used to elucidate what we might expect to be happening if and where Hector's dolphins are experiencing nutritional stress.

Results

The information available on wild dolphin diet generally comes from two main methods of data collection that are designed to gather different types of information:

1. The first relies on the analysis of stomach contents; and
2. The second focuses on identifying certain stable isotopes and fatty acids in the prey of a dolphin population and in the animals themselves (typically from bone collagen, skin or blubber of the animals).

Stomach content analysis is one of the oldest techniques used to study dolphin diet. Typically, this involves identifying species present in the stomach of dolphins that have been recovered for necropsy, usually individuals that have been bycaught or beachcast (washed up on shore). Contents of the stomach are washed through a sieve and then remains are examined and identified. Items usually found in dolphin stomachs include otoliths (ear bones) and teeth of fish, beaks (mouth parts) of cephalopods and sometimes the exoskeletons of crabs or other crustaceans. Once the contents have been separated, they can usually be identified as having belonged to a particular species. Items can also be measured to provide estimates of the size of the prey item when it was consumed and before it was digested. This method can potentially provide information on the species, size and quantity of each prey type consumed by the dolphin.

Identifying stable isotopes, including $\delta^{13}C$ and $\delta^{15}N$, in the tissues of dolphins and comparing these to the signatures of potential prey is a much more recent method for learning about dolphin diets. Since prey species that inhabit different parts of the water column have different isotopic signatures, this method can provide information on where in the water column the dolphins have been foraging. Unlike the specific prey species and sizes that can be identified through stomach content analysis, this latter method ideally identifies whether an individual dolphin has been feeding on prey in the surface waters (epipelagic), on the seafloor and throughout the water column (benthopelagic), and/or on or near the seafloor (demersal). However, stable isotope analysis is only useful if relative prey contributions can be accurately estimated from isotopic composition and prey species are correctly attributed to a place in the water column. Therefor caution must be exercised when interpreting these types of results.

Hector's/Māui dolphin diet

Almost all of what is currently known about Hector's and Māui dolphin diet comes from a Ph.D. thesis and a publication by Elanor Miller of Otago University (Miller et al. 2013; Miller 2014). As part of her work, she estimated the species, sizes and quantity of prey consumed by analysing the stomach contents of 63 Hector's dolphins obtained between 1984 and 2006. She also used stable isotope analysis, comparing $\delta^{13}C$ and $\delta^{15}N$ signatures in 42 dolphins and 19 potential prey species, to look at dietary preferences relative to epipelagic, benthopelagic and demersal foraging habitat.

Dolphins were obtained from four of the five known areas where genetically distinct subpopulations are found including South Island East Coast (SIEC), South Island West Coast (SIWC), South Island South Coast (SISC) and North Island West Coast (NIWC). No dolphins

from the South Island North Coast (SINC) were included. An overview of this important work is provided to summarize what is currently known regarding Hector's dolphin diet.

Stomachs contained remains of 22 species of fish (95%) and small numbers of cephalopods (2 species) and crustaceans (5 species). The average stomach contained the remains of 24 prey species, demonstrating that the diet of Hector's dolphins is diverse with prey species. A list of all prey identified, including reconstructed mass and length is included as Appendix I.

Of the stomachs examined, more than half (59%) contained red cod (*Pseudophycis bachus*) and 49% contained ahuru (*Auchenoceros punctatus*). These were the most prevalent species found, followed by arrow squid (*Nototodarus* sp.), sprat (*Sprattus* sp.), sole (*Peltorhamphus* sp.) and stargazer (*Crapatalus* sp.). Red cod, sole and ahuru occurred in stomach contents from all four areas where samples were found and all but the NIWC contained arrow squid. Javelinfish was only found in samples from the SIWC.

Figures 1 – 4 illustrate the percent mass contribution of species found for females, males and those of unknown sex, for each of the subpopulations. Note the difference in sample size for each area (SIEC n=36, SIWC n=23, SISC n=2, NIWC n=3). When amounts detected were less than 0.5% they were not represented in these figures.
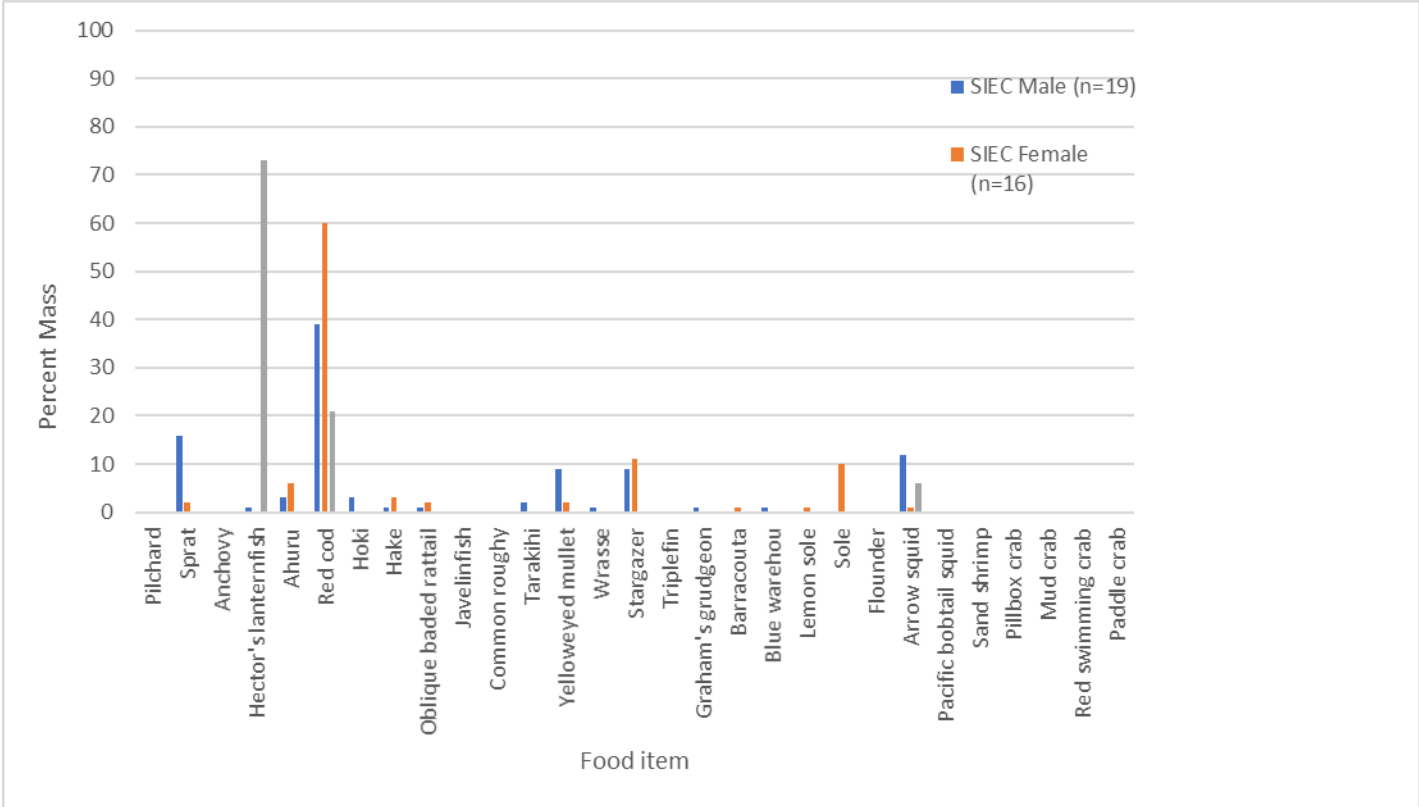

Figure 1. Food items identified in stomach contents of 36 Hector's dolphins from the South Island East Coast population depicted as percent mass (%M) for males, females and those of unknown sex.

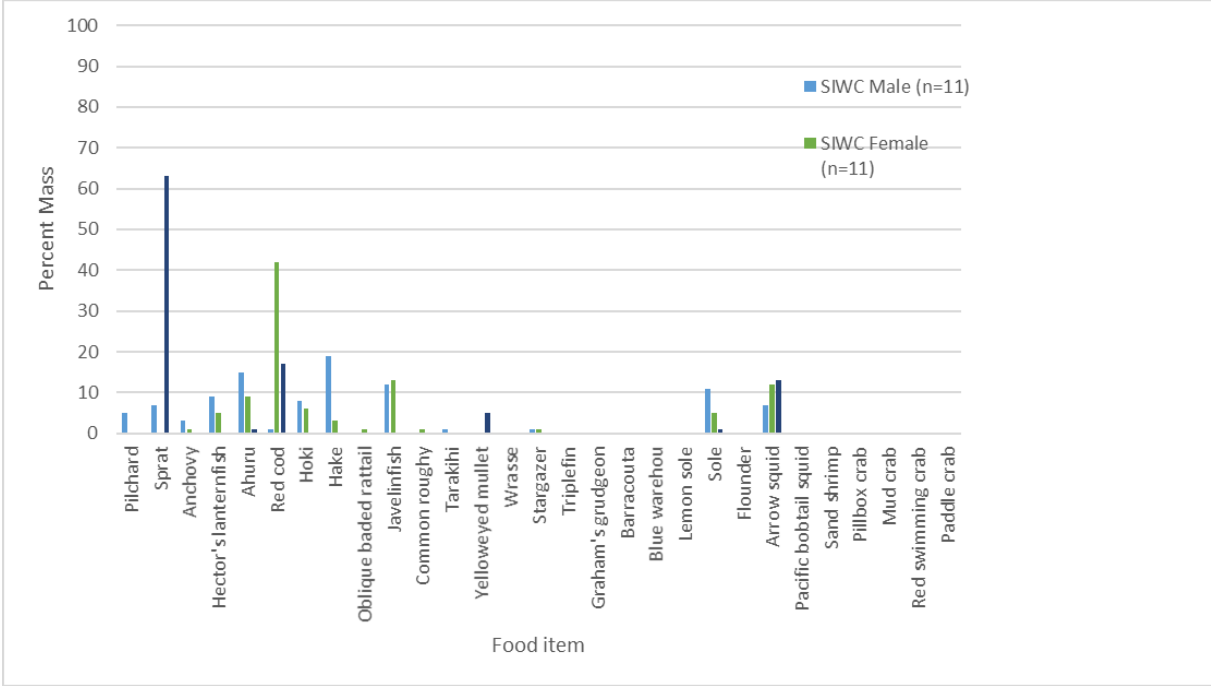Figure 2. Food items identified in stomach contents of 23 Hector's dolphins from the South Island West Coast population depicted as percent mass (%M) for males, females and those of unknown sex.
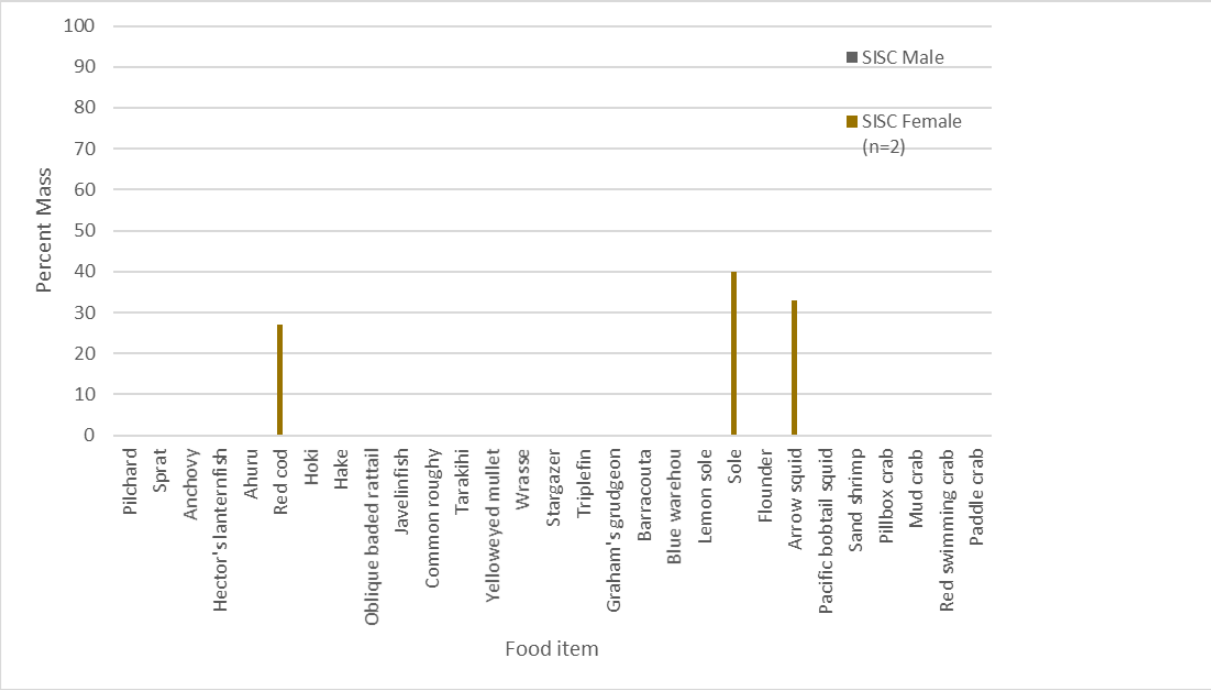

Figure 3. Food items identified in stomach contents of 2 female Hector's dolphins from the South Island South Coast population depicted as percent mass (%M) for males, females and those of unknown sex.
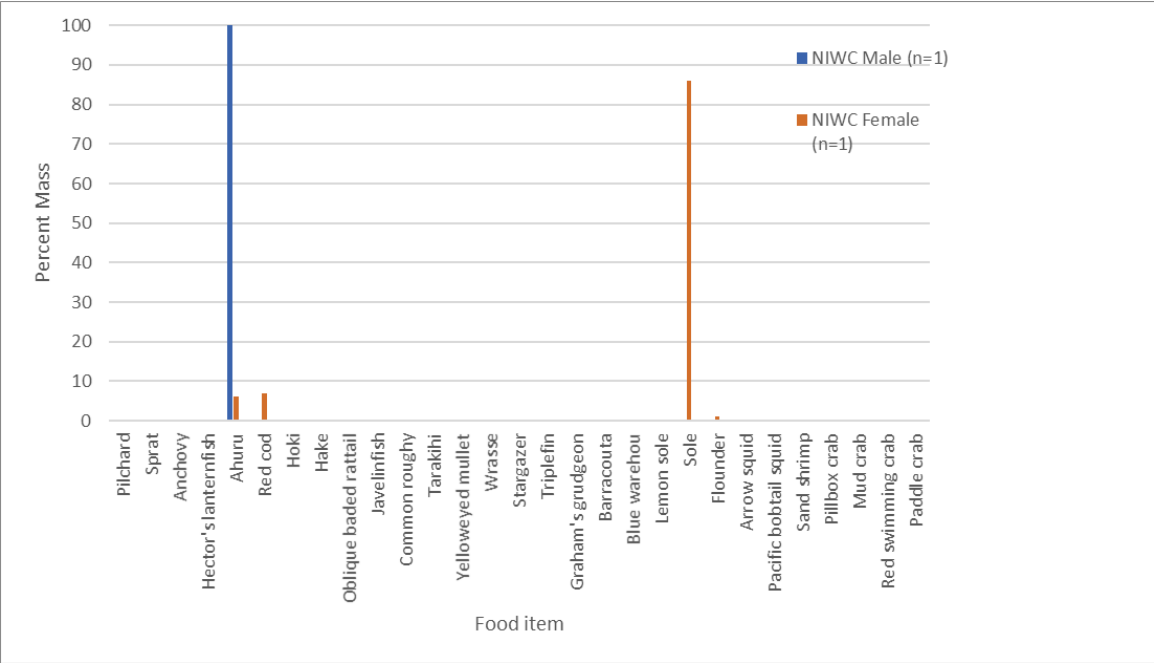
Figure 4. Food items identified in stomach contents of 1 male and 2 female Hector's dolphins from the North Island West Coast population depicted as percent mass (%M) for males, females and those of unknown sex.

Of the species identified, ahuru and Hector's lanternfish (*Lampanyctodes hectoris*) were found in the greatest numbers overall, while red cod made up the greatest component by mass. Figure 5 shows the percent mass of red cod from all available samples.

Figure 5. Red cod identified in stomach contents of Hector's dolphins from all four areas depicted as percent mass (%M) for males, females and those of unknown sex. Note the difference in sample size for each area.
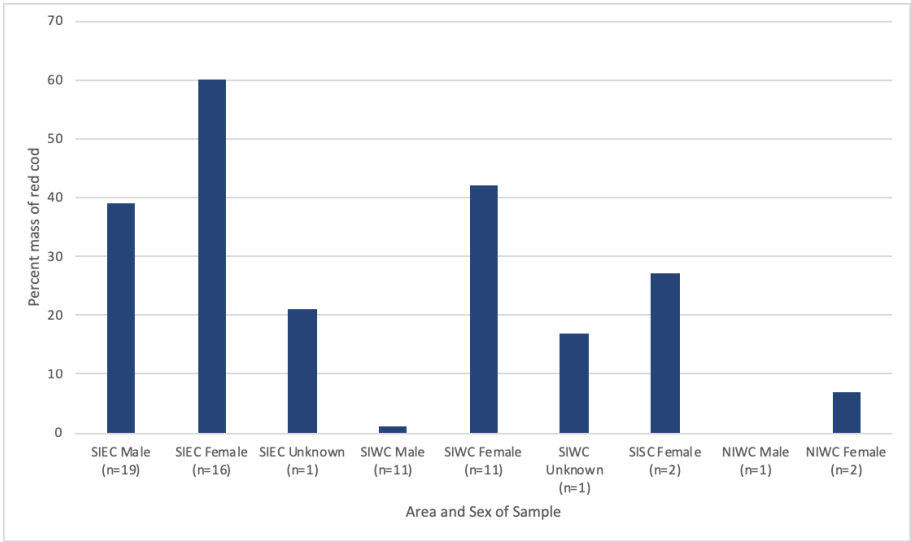
Most of the prey identified was estimated to measure less than 10 cm when consumed. However certain prey species, including pilchard (*Sardinops neopilchardus*), yellow-eyed mullet (*Aldrichetta forsteri*) and rattail (*Coelorinchus aspercephalus*) were often over 10 cm. Figure 6 illustrates the estimated mean length of the six species most commonly found in the stomachs of Hector's dolphins. Reconstructed mean lengths and SD in cm were as follows: red cod 17.9±10.1, arrow squid 17.1±9.4, sprat 10.4±2.1, stargazer 10.2±4.1, ahuru 8.3±3.3 and sole 4.4±4.0.
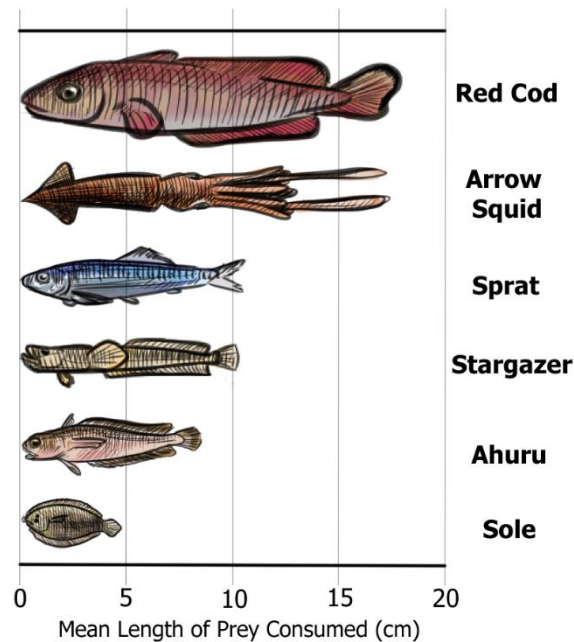

Figure 6. Estimated mean lengths of the six species most commonly found
in the stomachs of Hector's dolphins using reported lengths in Miller et al. (2013).
Drawn by Katie Eshelman

Since energetic demands and foraging and feeding ability and competency can vary by sex, age and reproductive status, we would also expect diets to vary between individuals within the same habitat. For example, a less experienced juvenile might feed on prey that is easier to catch while they develop their skills. A pregnant or lactating female that has different energetic and nutritional needs (discussed below) may seek out certain prey species that help her meet these requirements. When a female is accompanied by a calf, she is also limited in the distances she can travel to find food, and possibly the depths she is able to dive to.

Miller (2014) did find some variation in prey composition by age and sex. For example, on the SIEC, 38% of female stomachs contained stargazer and sole, whereas only 21% of males contained stargazer and none contained sole. Males in both the SIEC and SIWC contained more sprat than did females in both of the areas (26% vs 19% in SIEC and 45% vs 18% in SIWC). Red cod appeared to be more important by mass to females than to males in these two areas

where the most dolphins were sampled, in particular in SIEC (60% vs 39% in SIEC and 36% vs 27% in SIWC, see Figure 5).

While there is currently not enough data to describe the juvenile diet of Hector's dolphins, there is some information on the lactation period and first foods consumed by calves. Miller (2014) found six dolphins measuring 77 – 90 cm containing only milk in their stomachs and one measuring 99 cm containing milk and the remains of arrow squid. This suggests that until calves reach at least 90 cm, they are completely dependent on their mothers for nourishment. It also suggests that arrow squid may be particularly important as one of the first solid foods consumed by Hector's dolphin calves. No dolphins measuring longer than 107 cm had milk in their stomachs, indicating that by this length offspring must be competent in capturing prey to meet their own energetic requirements (Miller 2014).

Although only a very small sample size was obtained from the NIWC, where Māui dolphins occur, the stomach contents of the few animals found contained ahuru, red cod, sole and flounder in their stomachs. All but the flounder were also found in Hector's dolphins around the South Island.

Nutrition and Reproduction

The next step is to assess what conditions might lead to nutritional stress and how this stress, in turn, might influence reproductive success and thus population recovery and resilience.

The distribution and abundance of dolphins may be influenced by humans directly (for example by entanglement and mortality in fishing nets) or indirectly through what are referred to as indirect effects such as by influencing the distribution and abundance of their known prey species.

Hector's dolphins are small and have a low mass to surface area ratio, measuring a maximum of 146 cm and 45 kg, while Māui dolphins are only slightly larger, reaching at least 152 cm and 65 kg (Dawson 2009). This, combined with the fact that they inhabit temperate (i.e. cool) waters and move around almost constantly within their small home ranges, suggests that they have a high metabolic rate, similar to the physiologically similar Commerson's dolphin (Kastelein 1993).

To survive, individuals must meet these energetic demands by acquiring energy at a similarly high rate. In order to meet their energetic demands, Hector's dolphins likely need to acquire prey within relatively small (>30 km) and short (daily) scales (Williams and Maresh 2016). What we know of their small home ranges and daily movement patterns (Bräger and Bräger 2018) supports this assumption.

Ideally, within their home ranges, Hector's dolphins have access to abundant, high-energy prey within small areas and within short time scales. In other words, they are able to feed frequently throughout the day and don't have to travel far between meals. However, if adequate prey becomes less available, the energetic cost of acquiring it (including searching, detecting, chasing, capturing and digesting) will increase (Costa and Maresh 2017).

In the simplest sense, nutritional stress may occur when a dolphin spends marginally less or more energy acquiring prey than is obtained from the prey that they eat (Villegas-Amtmann et al. 2015). In Kastelein's study of captive Commerson's dolphins, individuals that did not eat, even for only a day, exhibiting notable weight loss (Kastelein et al. 1993).

This nutritional stress, in turn, may negatively impact reproductive success of individual females. Ultimately, mortality or reproductive failure from nutritional stress could contribute to population decline. Understanding how specifically nutritional stress might manifest in local populations of Hector's dolphin might help us identify if and how it is a factor to consider in population recovery.

More importantly, understanding the conditions where Hector's dolphins might be most susceptible to nutritional stress will aid us in identifying conservation and management actions to reduce threats and promote population recovery and resilience.

How does nutritional stress impact reproductive success?

Even once a dolphin finds, captures and ingests its prey, it is not capable of extracting all the chemical energy contained within that prey. After the non-digestible portion of what is consumed is lost as faeces, there is a smaller amount of energy that remains, referred to as the assumed digested energy (Costa and Maresh 2017). In marine mammals that eat fish, approximately 88 – 98% of the energy within their ingested prey is assimilated and thus available (Costa and Williams 1999).

Of this available energy, some is lost as heat output and a portion will be needed to cover the energetic cost of finding and capturing prey. A large amount will be used for metabolism and synthesis, basal metabolic rate (BMR), thermoregulation and activity (Costa and Maresh 2017). After these costs have been covered, what energy remains is used for growth, storage, reproduction and repair. All these energetic needs must be satisfied before energy can be available for producing and raising offspring.

In male Hector's dolphins, energy is required to find and mate with females. The energetic cost of reproduction for females is considerably greater and can be broken down into three main components: gestation, lactation and infant carrying.

Gestation: Since Hector's dolphins must be capable of swimming and surfacing to breathe immediately after birth and be able to cope with the high heat conductivity of the water around them, they must be born larger (relative to the size of the mother) and more developed than most terrestrial mammals. Gestation is therefore longer (approximately 10 – 11 months (Dawson 2009) than similarly sized terrestrial mammals with calves measuring 60 – 75 cm and weighing 8 – 10 kg at birth (approximately one quarter the weight of their mother, Slooten and Dawson 2013).

Lactation: The milk produced by marine mammals is more rich in fats than milk produced by terrestrial mammals and more dense in energy than the prey items consumed by the mother (Costa 1991). Dolphin calves suckle frequently and for short amounts of time on this nutrient

rich milk. Mothers continue searching for, capturing and ingesting prey between suckling bouts to meet their own energetic needs and those of their offspring. This strategy is known as 'income breeding' and allows offspring to grow quickly and develop the blubber layer they will need to survive in cold water (Costa and Maresh 2017). In Kastelein's study of captive Commerson's dolphins, females ate significantly more in the first 1 – 2 months after giving birth while the calf developed a thicker layer of blubber to help reduce heat loss through conduction (Kastelein et al. 2013).

Infant carrying: While not as obvious as the infant carrying of primates, dolphin mothers have an energetic cost when their offspring is swimming in either echelon or infant-position. This has been demonstrated in studies of captive bottlenose dolphins, where tail beats per minute were shown to increase for mothers and decrease for calves while swimming in this position (Noren et al. 2006, Noren 2008, Noren and Edwards 2011). This was also described for captive Commerson's dolphins, as mothers swim near constantly and 'pull' calves along with them in the slip stream (Kastelein et al. 1993).

As the calf gets bigger and more active their energetic needs increase and the costs of lactation and infant-carrying steadily increase for the mother. Throughout the calf rearing stages, the mother must continue to balance the costs of searching and diving for food and taking care of her dependent calf, while still meeting her own basic energetic needs. If she is unable to find sufficient and adequate prey within short time scales and small areas, the resulting nutritional stress could contribute to pregnancy failure or calf abandonment and/or mortality.

While we currently lack data on pregnancy failure or energy budgets for Hector's dolphins, we can infer how nutritional stress might be expected to influence Hector's dolphins by comparing to what has been found for other species. In the following sections, I will summarise four case studies with comparable components.

Comparative Case Study: Commerson's dolphins

As previously mentioned, Commerson's dolphin (*Cephalorhynchus commersonii commersonii*), is another member of the *Cephalorhynchus* genus and one which exhibit similarities, both physically and behaviourally to Hector's dolphins. Similar to Hector's dolphins, Commerson's dolphins feed throughout the day, and often only 3 – 5 m from shore and in shallow harbours (Gewalt 1990).

From studies of the stomach contents of wild animals, found around southern Chile, southern Argentina, the Falkland Islands and the Kerguelen Islands we know that their natural diet is also similar to that of Hector's dolphins, including small fish, including sprat, as well as squid and other invertebrates (Kastelein et al. 1993). In one study that examined stomach contents from individuals caught in the trawling nets in northern patagonia, hake contributed most to stomach contents, followed by the shortfin squid (Crespo et al. 1997). More recently, isotopic comparisons showed no differences between males and females but did demonstrate a significant dietary shift between juveniles and adults, with pelagic sprat in the diets of juveniles significantly more prevalent than it was in the diets of adults, while benthopelagic species were more prevalent in the diets of adults (Riccialdelli et al. 2013).

The most informative study for the purposes of comparison with New Zealand's Hector's dolphins is one that involved monitoring the food intake of 32 captive Commerson's dolphins from 5 separate zoological parks and estimating food consumption by mass and by energy (Kastelein et al. 1993). Although captive studies do not give precise replication of conditions in the wild, the findings of this study do offer a good baseline from which we can predict how Hector's dolphins might need to meet their energetic demands in the wild.

In the study by Kastelein and colleagues, adult males (weighing 29 – 54 kg) ate 8.1 – 13.5% of their body mass per day which was similar to non-pregnant adult females (weighing 32 – 53 kg) that ate 7.5 – 13.1% of their body mass per day. This equates to each adult dolphin in the wild requiring the equivalent of 1850 kg of herring or 37×10^5 kcal per year. This confirmed that Commerson's dolphins do have a very high metabolic rate, owing mostly to their low body mass to surface ratio and their need to constantly move and feed in order to maintain body condition. It also gives us an idea of how much might be required to sustain a Hector's dolphin.

Commerson's dolphin calves ate between 6 and 10% of their body weight per day, and the time that calves were completely reliant on milk for nutrition ranged from 73 – 236 days. During this period of complete nutritional dependency, mothers consumed approximately 30% more food each day than during times when she was not pregnant or lactating.

The authors of this study concluded that females require a particularly large food supply when they are lactating and predicted that Commerson's dolphins cannot survive several days without feeding. They suggest that their small home ranges might be due to their energetic inability to travel long distances without acquiring prey.

Comparative Case Study: Southern Resident Killer Whales

In Hector's dolphins, as in most dolphins, the way we know that a female has been pregnant is when we see her with a calf. However, the number of pregnancies that fail, through spontaneous abortion, premature birth, still birth, perinatal or neonatal mortality, remains unknown.

A long-term study of pregnancies in southern resident killer whales (*Orcinus orca*) by Wasser and colleagues (2017), summarized below, provides insight of how inadequate nutrition could potentially contribute to population decline in Hector's dolphins.

In this study, researchers collected southern resident killer whale (SRKW) faeces samples from known animals over a six-year period (2008 – 2014) using trained detection dogs. They subsequently measured levels of progesterone and testosterone metabolites within the samples to assess pregnancies and thyroid and glucocorticoid hormone metabolites to assess physiological stress. From regular monitoring, they were able to determine that 69% of the pregnancies that were detected failed, and that roughly half of these failures occurred in the later stages of pregnancies. The patterns detected in the hormone profiles also demonstrate that SRKWs are experiencing periodic nutritional stress and that this stress is associated with the very high rate of pregnancy failure. The authors assert that pregnancy failure is a major constraint on killer whale population growth and that these pregnancy failures are 'triggered by insufficient prey'.

SRKW primarily rely on Chinook salmon between May and October. From November through April (the winter months in the northern hemisphere), their prey is dispersed over larger areas and tends to be generally smaller in size. Since winter is also the time of year when the water is the coldest, it is presumed that energetic demands might be more challenging to meet during this period. For these reasons, it is especially important that big, fatty, nutrient rich runs of salmon are available to SRKW in the early spring and then again in late August, to compensate for the leaner times in the winter. Since SRKW are pregnant for 18 months and calves are typically born in the winter, both conception/early term and the latest term of the pregnancy occur during the May – October period, at the time when salmon was historically plentiful, but has dramatically declined in recent years.

There are some comparisons that can be made to this case to help us to speculate what could potentially happen to a population of Hector's dolphins if nutritional stress were a factor. The gestation of Hector's dolphins lasts approximately 10 – 11 months. Conception usually occurs in summer or early autumn and females give birth in late spring or summer. For a female to meet the energetic demands of her growing foetus, she must obtain sufficient food to meet her own needs and the needs of the foetus. If we assume that the winter months are when prey is more widely dispersed and when water temperatures are cooler, we might expect females to be more at risk of pregnancy failure if the abundance and/or distribution of their prey means that they aren't able to meet all these energetic demands at this particular time of year.

Comparative Case Study: Sea otters

While the previous case study provides information on how nutritional stress may indirectly influence population growth through pregnancy failure, the following study demonstrates how the small size and income breeding strategy of Hector's dolphins might make them especially susceptible to nutritional stress in the period between birth and independence.

Rather than a thick layer of blubber, sea otters (*Enhydra lutris*) rely on an especially high metabolism (i.e. they eat all the time) and their fur to thermoregulate in temperate waters. While they don't have fur, we can expect a similarly small Hector's dolphin to need a high metabolic rate and to eat all the time to effectively thermoregulate as well. This high metabolic rate is energetically costly to maintain and requires frequent feeding on high energy prey to sustain, in both males and females. In females, these and other basic costs must be met before energy can be spent on pregnancies and subsequent lactation and infant care.

In 2014, Thometz and colleagues published a study illustrating how a reduction in sea otter prey along the central California coast contributed to high rates of mortality in dependent pups, juveniles and reproductive females.

By calculating the energetic demands of pups at different stages of development, the authors were able to demonstrate that when her pup is three weeks old, the daily energetic demands on a sea otter mother are 17% higher than energy demands pre-pregnancy. Even more remarkable is that her daily energetic demands are 96% greater (than energy demands pre-pregnancy) around the time her pup is weaned.

Like Hector's dolphins, sea otters are income breeders. Since they are not capable of building up fat reserves, they must balance the costs of lactation and infant carrying by increasing the amount of food that they consume and foraging regularly between bouts of suckling and infant carrying.

It is not surprising then, that female sea otters lose weight throughout lactation (Monson et al. 2000) and that those with poor body condition are the ones that lose their pup through mother-pup separation (Garshelis and Garshelis 1987).

Sea otter populations have been slow to recover in some areas, despite the elimination of direct threats such as hunting. The authors suggest that high mortality rates in pups and in females at the time of weaning (termed 'end-lactation syndrome') are being exacerbated by the reduced abundance of suitable prey in the area (Tinker et al. 2008).

While energy budgets have not been studied specifically in Hector's dolphins, we know that one of the causes of death that is documented for calves is maternal separation (Roe et al. 2013). It is possible that some of these cases might be related to nutritional stress due to the high energetic demands on the mother.

Comparative Case Study: Yellow-eyed penguins and red cod

As was seen in the example of killer whales provided above, there are often particular prey species that are proportionately more important than others. In the case of the southern resident killer whales, their annual movement and feeding patterns all revolve around the life cycle of Chinook salmon. Now that this food source is less abundant and less predictable, SRKW are facing nutritional stressors which are likely contributing to population decline.

The work done by Miller demonstrated that red cod was of particular importance to the diet of Hector's dolphins between 1984 and 2006. This particular prey item was present in 59% of the stomachs examined and made up the greatest single proportion (37%) of the overall mass of prey consumed (Miller et al. 2013). The offshore shift in Hector's dolphins in the winter months was also theorised to be related to the offshore shift of red cod at this time of the year (Miller 2014). This evidence suggests that red cod may play a critical role as prey for Hector's dolphins.

In a recent review of yellow-eyed penguin diet and indirect effects, Mattern and Ellenberg (2018) described how red cod has historically been important for this critically endangered seabird as well. Their work illustrates that red cod went from being the largest contributor by mass in yellow-eyed penguin diet in the 1980s to the fifth largest contributor in the 1990s. Correspondingly, blue cod increased in importance and present-day animal-borne camera evidence suggests that blue cod (and opalfish) are now the main prey species taken. The authors predicted that the shift away from red cod as the main prey item may have been due to reduced red cod abundance in areas where yellow-eyed penguins are found. This decline is attributed in turn to a combination of rising ocean temperatures and human fishing pressure. However, trawl survey trends within the ECSI area specifically suggest that red cod abundance is not uniform along the entire coast and that it likely increases and decreases in different areas at different times (see Figure 9 in Beentjes et al. 2016). If red cod are less available overall for Hector's dolphins and if/how this might specifically impact them remains unclear at this stage.

In yellow-eyed penguins, the switch to blue cod, a larger prey species, has meant that chicks are sometimes unable to ingest the prey that their parents bring home. The energetic cost of capturing blue cod also appears to be markedly greater than the cost of capturing smaller prey.

While a diet shift away from red cod has been detected in yellow-eyed penguins, we currently don't have the data to understand if and how the role of red cod in the diet of Hector's dolphins has changed over time. However, we can expect that if there is less red cod available, that this will influence Hector's dolphins in some way. The dolphins might need to travel farther to find enough red cod or they may have shifted to another main prey item that is more readily available but not necessarily as nutrient or calorie rich. Either of these scenarios would have energetic consequences for the dolphins and might contribute to various forms of nutritional stress.

While the activities of fisheries will alter the abundance and distribution of Hector's dolphin prey, it is difficult to ascertain where and when a threshold is breached and nutritional stress occurs.

Diet and dolphin diseases

Nutritional stress could also be affecting dolphin survival and reproductive success if it compromises the animal's immune system thus rendering it more vulnerable to infection and disease.

For example, necropsies performed on Hector's and Māui dolphins found that *Toxoplasmosis gondii* was the cause of death in 25% of cases, while 60% of the animals tested positive for the presence of *T. gondii* DNA (Roe et al. 2013). This implies that in most cases where *T. gondii* is present, it is latent and not related to the cause of death. If, however, the dolphin was experiencing nutritional stress in some form due to insufficient or inadequate food, *T. gondii* is more likely to become active and cause either direct mortality, pregnancy failure or detrimental behavioural changes that increase the risk of predation (Roe et al. 2013).

Similarly, *Brucella* was present in 37% of 27 Hector's dolphins remains that were tested, but only active in 7% (Buckle et al. 2017). In the cases where it was active, the animals died of reproductive disease due to *Brucella* infection (Buckle et al. 2017).

Summary of key points and conclusions

In summary, many of the physical and behavioural characteristics of Hector's dolphins make them particularly vulnerable to nutritional stress and the associated consequences.

They are small. Hector's dolphins measure a maximum of 146 cm and 45 kg, while Māui dolphins can reach at least 152 cm and 65 kg (Dawson 2009). Their smaller size means that they must obtain food regularly, preferably within small areas and short timeframes, to keep up with their fast metabolism.

They live in cold water. Hector's dolphins have a high surface to volume ratio, meaning that they will experience more heat loss to the surrounding environment. More energy is required to compensate for this loss.

They produce big calves. When calves are born they measure $60 – 75$ cm and weigh $8 – 10$ kg (Slooten and Dawson 2013), which is approximately one quarter the weight of their mother. While this large birth size is necessary to ensure that the calf can swim and surface on its own within seconds of being born, the high costs associated with the development of calf are borne by the mother. Photoidentification work with known individuals indicates that females likely produce one calf every $2 – 4$ years (Dawson 2009) but little is known about how long calves are dependent on their mothers. We can surmise however that the investment by the mother is considerable and that she will need to be able to obtain additional prey to meet these energetic demands (as has been shown for Commerson's dolphins, Kastelein et al. 1993).

They are income breeders. Again, owing to their small size and their inability to store energy as fat, females employ an income breeding strategy, where they must continuously feed throughout pregnancy and lactation to meet their energetic demands. If females must travel too far to find suitable prey, they likely will not be able to meet these demands and would be likely to experience nutritional stress.

They are often found close to shore. This presumably makes Hector's dolphins more susceptible to pathogens and diseases that come from terrestrial sources and human activities that impact the nearshore environment. If suffering from nutritional stress, toxoplasmosis and brucellosis can be especially lethal.

They show preference for localised physical areas known as hotspots. These places seem to be especially important foraging spots for Hector's dolphins (Brough et al. 2018).

Many of their preferred prey is currently captured in trawl fisheries, either as targeted species or as bycatch (Beentjes et al. 2016). Red cod, one of the most important prey of Hector's dolphins, may have declined in abundance within some areas where Hector's dolphins are found.

While the very nature of an indirect effect makes it impossible to pinpoint, from the characteristics above and the comparative case studies considered, we can expect that:

1. Hector's dolphins are particularly susceptible to nutritional stress,
2. nutritional stress will most obviously manifest as fewer calves being born and/or surviving to independence,
3. areas where we see the largest densities of Hector's dolphins could also be important for prey species
4. any human activity that reduces the abundance of Hector's dolphin prey is potentially contributing to nutritional stress.
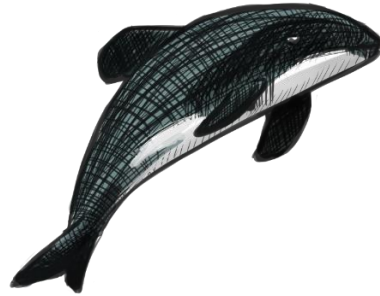
Recommendations for future research

Although there have been no studies that look at the specific energetic challenges that Hector's dolphins must overcome to survive and reproduce, what we do know about their physiology and behaviour and the consequences of nutritional stress in other species tends to support the assumption that it plays a role in reproductive success.

Following is a list of recommendations for research that will improve our understanding of Hector's dolphin ecology and be useful for informing conservation and management actions (management to reduce threats and promote population recovery and resilience).

1. Identify the locations and approximate sizes of hotspots throughout Hector's dolphin habitat and monitor prey in these areas.
2. Describe the spatial distribution of Hector's/Māui prey and temporal variation in their abundance in areas foraged by Hector's/Māui dolphins (and of a comparable size fraction to those predated)
3. Conduct research to understand how climate/fishing might contribute to past temporal trends (in the point above) and future prey availability (e.g. what can we learn from the marine heatwave year?, where is fishing intensity highest and how might this impact on availability or the right size fraction?).
4. Develop a HD camera and GPS dive tracking device that could be temporarily attached to a Hector's dolphin using a suction cup. These types of devices have revealed a wealth of information regarding the prey and feeding behaviours of yellow-eyed penguins (Mattern and Ellenberg 2018) and the suction cup technology has been successfully trialled in dusky dolphins off Kaikōura (Pearson et al. 2017).
5. Collate existing data on calving rates in known individuals and estimate whether these rates show variation by location or by year. A better understanding of reproductive rates around the country will indicate if particular areas are more subjected to nutritional stress.
6. Employ techniques that assess potential cumulative effects, including the presence of disease and toxins in known Hector's dolphin hotspots. For example, mussels have been used as an indicator of toxoplasmosis presence or absence in coastal environments. Understanding where and when habitats are affected could help to focus efforts to reduce or eliminate specific human activities that may be contributing to the problem.

7. Continue to assess the stomach contents of any Hector's dolphins that are necropsied. It would be valuable to determine whether the diet has changed in the 12 years since the last sampling took place.

Acknowledgements

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Appendix I. List of prey identified by Miller, including reconstructed mass and length. Data were collected from the diagnostic remains of 63 stomach contents of Hector's dolphins bycaught and beachcast throughout New Zealand 1985 – 2006. Used with permission.

Prey		*n*	Mass (g) Mean ± SD	Min	Max	Length (cm) Mean± SD	Min	Max
FISH								
Sardinops neopilchardus	Pilchard	9	24.6 ± 9.4	11	41	13.3 ± 1.7	11	16
Sprattus sp.	Sprat	86	12.1 ± 13.0	2	91	10.4 ± 2.1	7	19
Engraulis australis	Anchovy	29	4.0 ± 1.9	2	8	7.8 ± 1.2	6	10
Lampanyctodes hectoris	Hector's lanternfish	365	2.1 ± 0.9	0.7	7	5.9 ± 0.7	4	9
Auchenoceros punctatus	Ahuru	520	4.0 ± 3.8	0.1	20	8.3 ± 3.3	2	16
Pseudophycis bachus	Red cod	170	107.6 ± 135.6	0.1	830	17.9 ± 10.1	2	44
Macruronus novaezelandiae	Hoki	15	93.3 ± 63.8	2	266	28.9 ± 8.9	8	45
Merluccius australis	Hake	32	65.0 ± 64.6	4	313	20.0 ± 6.6	9	37
Coelorinchus aspercephalus	Oblique banded rattail	7	60.9 ± 33.3	16	104	23.1 ± 4.7	16	28
Lepidorhynchus denticulatus	Javelinfish	106	21.9 ± 28.1	0.1	162	18.6 ± 5.7	3	28
Paratrachichthys trailli	Common roughy	1	92.6	-	-	9.5	-	-
Nemadactylus macropterus	Tarakihi	15	12.4 ± 4.5	7	25	9.2 ± 1.0	8	12
Aldrichetta forsteri	Yelloweyed mullet	10	158.3 ± 107.3	20	302	21.0 ± 6.6	12	28
Notolabrus sp.	Wrasse	1	215.8	-	-	22.3	-	-
Crapatalus sp.	Stargazer	128	14.7 ± 25.1	0.8	128	10.2 ± 4.1	5	24
Forsterygion sp.	Triplefin	1	2.0	-	-	6.0	-	-
Grahamichthys radiata	Graham's gudgeon	160	0.5 ± 0.4	0.1	2	4.1 ± 0.6	3	6
Thyrsites atun	Barracouta	6	27.6 ± 14.9	3	44	18.2 ± 4.8	9	22
Seriolella brama	Blue warehou	4	28.2 ± 32.4	3	73	10.2 ± 4.5	6	16
Pelotretis flavilatus	Lemon sole	1	195.8	-	-	27.8	-	-
Peltorhamphus sp.	Sole	1,258	5.4 ± 48.0	0.1	1282	4.4 ± 4.0	0.5	50
Rhombosolea sp.	Flounder	1	37.0	-	-	18.6	-	-
CEPHALOPOD								
Nototodarus sp.	Arrow squid	75	48.3 ± 118.9	0.1	960	17.1 ± 9.4	3	61
Sepioloidea pacifica	Pacific bobtail squid	4	4.3 ± 1.8	2	6	1.8 ± 0.2	2	2
CRUSTACEAN								
Pontophilus australis	Sand shrimp	1	0.4	-	-	3.6	-	-
Halicarcinus sp.	Pillbox crab	46	0.1 ± 0.1	0.1	0.7	0.6 ± 0.2	0.3	1
Macrophthalmus hirtipes	Mud crab	3	2.5 ± 0.6	2	3	1.9 ± 0.2	2	2
Nectocarcinus antarcticus	Red swimming crab	1	0.2	-	-	0.9	-	-
Ovalipes catharus	Paddle crab	4	3.6 ± 5.7	0.2	12	2.1 ± 1.3	1	4