CSP16205-1 POP2016-05

Yellow-eyed penguin diet and indirect effects affecting prey composition

Collation of biological information

THOMAS MATTERN & URSULA ELLENBERG

Department of Conservation
Te Papa Atawhai

EUDYPTES
EcoConsulting

Table of Contents

Abstract

Even though the mainland population of Yellow-eyed penguins represents the most studied group of penguins in New Zealand, information about their prey composition is scarce. The bulk of the work to date has been conducted in the mid-1980s and early 1990s with more recent dietary information being very limited. However, data at hand suggest that a significant shift in the major prey species has occurred in the past 30 years where red cod, a dominant prey species in terms of frequency of occurrence and diet biomass at many sites in the 1980s, has been largely replaced by blue cod since the 1990s.

There is a considerable difference in size between red cod, that were predominantly caught during the larval and early juvenile stage (length: 50-80mm), and blue cod, which was consumed at significantly larger sizes (160-220 mm). This may affect the survival of penguin chicks which appear not be able to ingest such large prey. The shift from red cod to blue cod coincided with a substantial reduction in landings in the red cod fishery, with some indications that fishing pressure may have contributed to a depression of red cod stocks. It appears that fisheries-related disturbance of the Yellow-eyed penguins' benthic foraging habitat may have favoured blue cod, due to this species' relative tolerance to fishing disturbance leading to an apparent increased availability in fished areas.

There are regional differences in Yellow-eyed penguin diet composition. In regions where seafloor habitats are defined by coarse sand and gravel penguin diet is dominated by opalfish, while in regions with structured benthos (e.g. biogenic reefs, horse mussel fields) but also seafloors exposed to bottom fisheries, blue cod is a more important prey species.

There are clear indications that Yellow-eyed penguins from the New Zealand mainland are impacted by indirect effects of anthropogenic activities at sea, predominantly fisheries operations. However, the current knowledge of the Yellow-eyed penguins' diet composition and marine ecology in general is limited, which makes it difficult to assess the extent to which these effects contribute to the mainland population's current decline.

Keywords

Yellow-eyed penguins, diet composition, prey preferences, marine ecology, seafloor degradation, indirect fisheries effects

Introduction

Background/context

Determining the diet composition of penguins is not an easy task. There have been various approaches to analyse diet composition ranging from killing and dissecting birds to obtain their stomach contents (Lishman, 1985), the less drastic but still very invasive stomach flushing (Wilson, 1984), to the more recent analysis of stable isotope ratios in feathers or blood (Thompson et al., 2005) and extraction of prey DNA from faecal samples (Jarman et al., 2013). Most recently, the use of animal-borne high definition cameras has offered another approach that not only allows the determination of prey composition but also provides information about pursuit strategies, prey encounter rates and correlation of prey abundance and habitat structure (Mattern, 2016; Mattern et al., 2017a).

None of the non-lethal techniques provide truly quantitative measures of the diet composition. Stomach flushing provides mainly information about prey items not yet digested by the penguin which may result in biased analysis towards prey that either takes longer to digest (e.g. van Heezik & Seddon, 1989) or that has been ingested shortly prior to sampling (e.g. Mattern et al., 2009). The non-invasive analysis of prey DNA in scat samples provides broader information about prey species penguins obtained during a foraging trip, but does not allow the assessment of size classes of prey items and does not distinguish between primary and secondary ingested prey (Deagle et al., 2010). Stable isotope analysis integrates information about diet over longer time periods, but is not able to discriminate between prey species from similar trophic levels (Flemming & van Heezik, 2014). Animal-borne cameras are currently limited to short deployment periods of three to four hours (Mattern et al., 2017a). It is important to keep these limitations in mind when analysing variation in prey composition in any penguin species.

While the mainland population of Yellow-eyed penguins is the most intensively studied of all New Zealand's penguins, with research projects dating as far back as the 1930s, there are few studies of prey preferences. To date, there are four published quantitative accounts of the species' diet composition (van Heezik, 1990a,b; Moore & Wakelin, 1997; Browne et al., 2011); other publication use data sets already summarized these sources (van Heezik & Davis, 1990; Moore et al., 1995; Ellenberg & Mattern 2012).

Prey available to Yellow-eyed penguins play a major role in what determines the species' reproductive success (van Heezik & Davis, 1990; Browne et al., 2011) and subsequently population changes (Mattern et al., 2017b). Prey availability is primarily a function of the marine environment the penguins use for foraging. As principally benthic foragers (Mattern et al., 2007), Yellow-eyed penguins rely on an intact seafloor ecosystem that supports adequate biodiversity and prey abundance to sustain the local penguin populations. Alterations of benthic ecosystems likely affect Yellow-eyed penguins significantly, be it through climate change-related system-wide shifts (Boyd, 2011), increased sedimentation (e.g. McLeod et al., 2014), or fisheries-related habitat degradation (e.g. bottom trawling, dredging; Lokkeborg, 2005).

Objectives

This report collates data on Yellow-eyed penguin diet over the past decades to summarise regional, seasonal and inter-decadal differences in the prey composition of New Zealand's mainland population. The findings are discussed in the context of environmental factors with an emphasis on alterations of the marine habitat as a result of anthropogenic influences, particularly fisheries interactions, including both changing structures of local fish stocks as well as degradation of seafloor habitat.

Methods

Published as well as unpublished information was collated and, where possible, quantitative data were derived from tables in the published sources. If no tabular data were available, graphs were extracted digitally, imported into vector graphics software (Adobe Illustrator CS6, Adobe Systems Inc, Mountain View, California, USA) and values determined using pixel measuring tools. Means and standard deviations were derived from these reconstructed data using the total number of observations and back calculating the number of observations in each class. This process was necessary for van Heezik (1990a), i.e. fish length and regional diet composition (data derived from the graphs in Figure 1 and Figure 2 in van Heezik 1990a), and mass contribution of different prey species at Boulder Beach, Otago Peninsula and Long Point, Catlins (data extracted from Figure 3 in Moore & Wakelin, 1997).

Results

Detailed quantitative data on the diet composition of Yellow-eyed penguins are available from four published sources (van Heezik, 1990a,b; Moore & Wakelin, 1997; Browne et al., 2011); additional publications use the same data presented in these four papers (i.e. van Heezik & Davis, 1990; Moore et al., 1995).

van Heezik (1990a) provides the most comprehensive overview of the penguins' diet composition across most of their mainland distribution. A total of 512 stomach samples were collected from adult penguins between March 1984 and August 1986 at seven different sites, ranging from Moeraki, Shag Point and Bobbys Head in North Otago, Boulder Beach on the Otago Peninsula, Nugget Point, Penguin Bay and Hinahina Cove to Falls Creek which is today known as Te Rere (Figure 1). van Heezik (1990b) reports on the diet composition of Yellow-eyed penguins from Codfish Island/Whenua Hou when 12 adult and 10 juvenile penguins were stomach sampled in October 1984. Moore & Wakelin (1997) provide data derived from 198 stomach samples taken between February 1991 and December 1993 at Boulder Beach, Otago Peninsula and Long Point in the Catlins (Figure 1). Finally, Browne et al. (2011) report on stomach contents of 12 adult Yellow-eyed penguins breeding along the north-eastern coastlines of Stewart Island (Golden Beach & Rollers Beach) and 15 penguins from Codfish Island/Whenua Hou (Penguin Bay & Sealers Bay) sampled between November and December 2006.

Main prey species, inter-decadal & regional variations

Figure 1 provides a general overview of prey composition of Yellow-eyed penguins from the New Zealand mainland as derived from published accounts to date.

1980s

In the mid-1980s , three prey species dominated the Yellow-eyed penguins' diet: red cod (*Pseudyphycis bacchus*), opalfish (*Hemerocoetes monopterygius*), and sprat (*Sprattus antipodum*) made up on average nearly two-thirds of the penguins' stomach contents (van Heezik, 1990a; Figure 2). There were regional variations; for example, at Moeraki and Boulder Beach, opalfish was the most important prey species while red cod played only a very minor role. Yet at the other sites the opposite was true (Figure 1). Sprat,

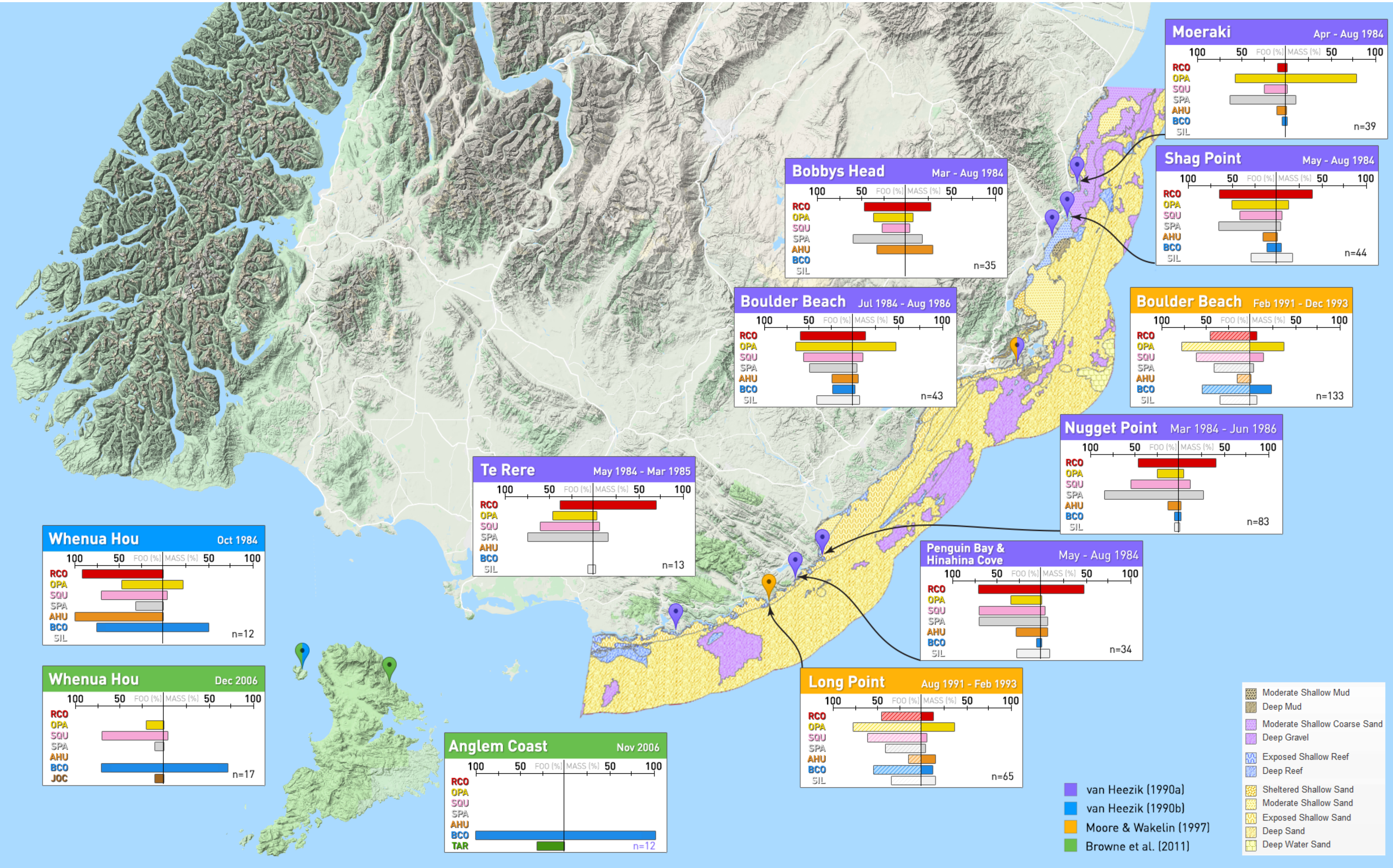

Figure 1. Summary of general prey composition in Yellow-eyed penguins between the 1980s and 201s. Each graph shows the frequency of occurrence of prey (left half of bar chart) and the relative mass contribution of each species (right half of bar chart) to the diet. Fish species are red cod (RCO, red), opalfish (OPA, yellow), sprat (SPA, grey), arrow squid (SQU, pink), ahuru (AHU, orange), blue cod (BCO, blue), silverside (SIL, light grey), tarakihi (TAR, green), jock stewart (JOC, brown). Colour of graph headers indicate the corresponding study these data derive from. Sediment distribution are reproduced from *https://www.seasketch.org/#projecthomepage/5331eff529d8f11a2ed3dd04*

red cod and opalfish were also the prey species most frequently found in the stomach contents. Arrow squid (*Nototodarus sloani*) was equally common (Figure 3), although the low biomass contribution of the cephalopod (Figure 2) indicates that it was caught in low quantities. Particularly noteworthy is that blue cod (*Parapercis colias*) was if relatively minor importance in mainland penguins' diet, but on Codfish Island/Whenua Hou blue cod made up more than 50% of the stomach content biomass (Figure 1, van Heezik, 1990b).

1990s

By the 1990s, the relative importance of blue cod had increased both in terms of relative biomass contribution and frequency of occurrence (Moore & Wakelin, 1997; Figure 1). At Boulder Beach, opalfish and blue cod made up 59% of the biomass brought ashore by the penguins. Red cod, however, was reduced to only a minor component (ca. 7% of the biomass). In the Catlins, opalfish had become the most important prey species (ca. 30% of the biomass) followed by ahuru (*Auchenoceros punctatus*), silverside (*Argentina elongata*), red cod and blue cod (8-13%).

Other prey species frequently observed were tarakihi (*Nemadactylus macropterus*) and triplefin (*Tripterygiidae*), which occurred in 29.4 and 36.9% of all samples, respectively, but contributed only small amounts of prey biomass (<3%) (Moore & Wakelin, 1997).

2000s

The study of diet composition on Stewart and Codfish Island in the mid-2000s found that blue cod was the single most important prey species in the diet of the penguins (Browne et al., 2011; Figure 1). On Stewart Island, only 9 of the 12 stomach-flushed penguins brought food ashore and with the exception of one bird that had caught a tarakihi, the rest preyed solely on blue cod. Prey diversity was more varied on Codfish Island/Whenua Hou than Stewart Island although three quarters of the food brought ashore consisted of blue cod.

2010s

Although no further quantitative studies of Yellow-eyed penguin prey have been published, the preliminary results of the analysis of animal-borne camera deployments on penguins from Boulder Beach in December 2016 (Mattern et al., unpublished data) indicate that blue cod and opalfish remain the main prey species caught by Yellow-eyed penguins foraging

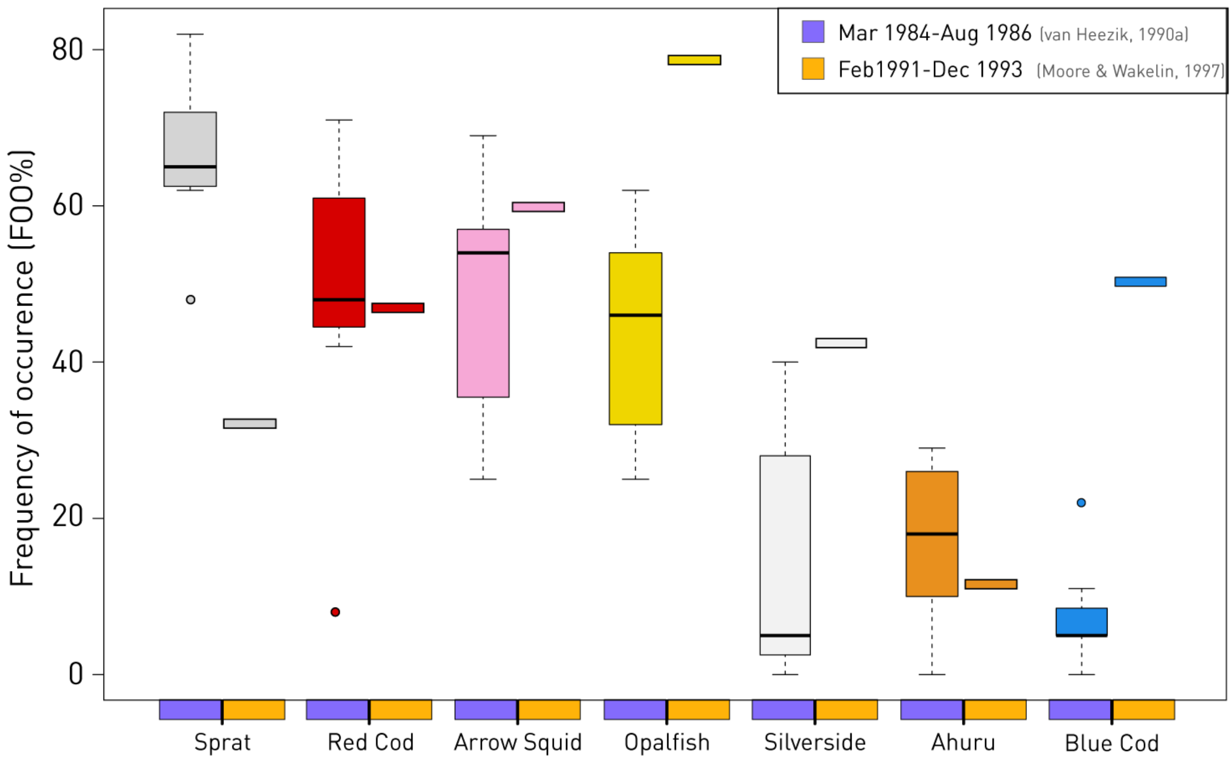

Figure 2. Median (for van Heezik, 1990a) and mean (for Moore & Wakelin, 1997) frequency of occurrence of the main Yellow-eyed penguin prey species in the 1980s and 1990s.

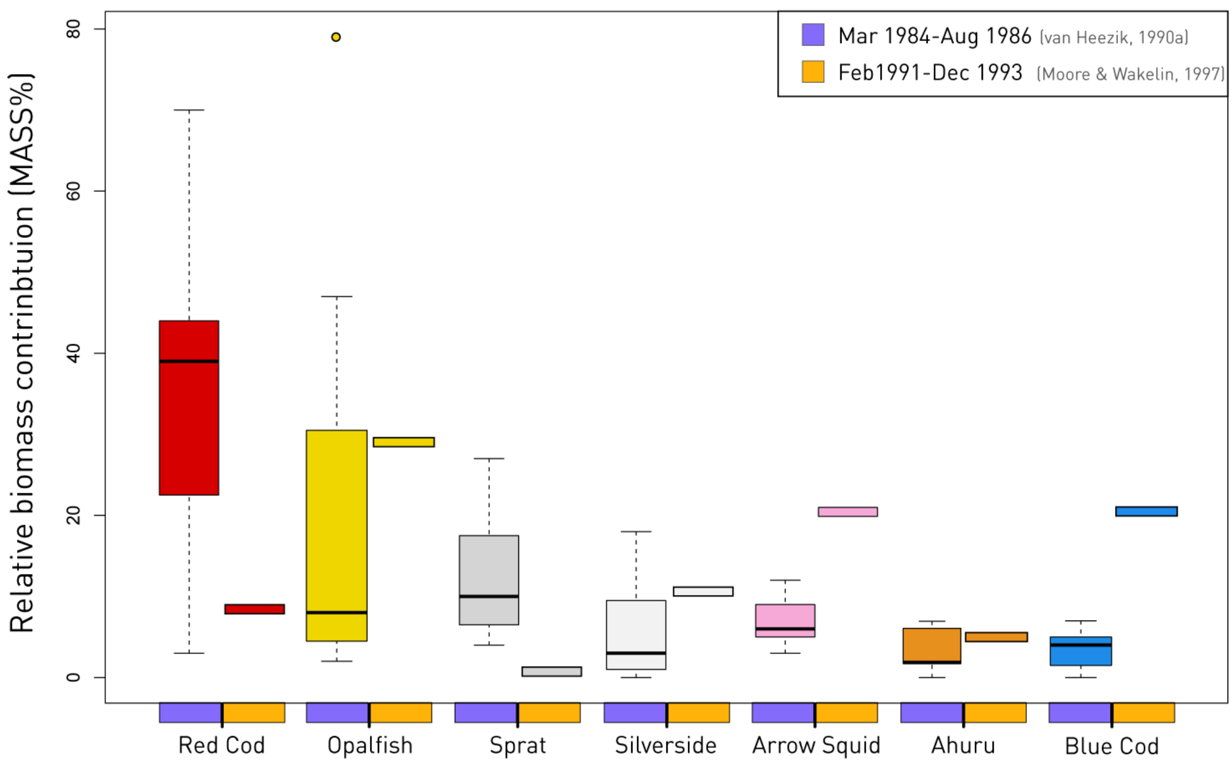

Figure 3. Median (for van Heezik, 1990a) and mean (for Moore & Wakelin, 1997) relative biomass contribution of the main Yellow-eyed penguin prey species in the 1980s and 1990s.

at the seafloor (frequency of occurrence [FOO] - opalfish: 61%, blue cod: 24%, sprat: 6%, tarakihi: 3%, n=4 penguins, ca. 9 hours of video footage). The substantial size difference between blue cod and opalfish (mean body mass – blue cod: 94.3 ± 74.4g, n = 247; opalfish: 26.6 ± 20.6g, n = 131; Moore & Wakelin, 1997) makes it likely that the bulk of the prey biomass consists of the former species (see *https://vimeo.com/179414724*).

Video footage recorded on eight yellow-eyed penguins breeding along the Anglem coast/Stewart Island in December 2016 indicates that penguins nesting at Golden Beach (S46.802°, E168.020°) fed mainly on juvenile tarakihi, sprat and in some instances on jock stewart (*Helicolenus percoides*), whereas birds from Rollers Beach (S46.768°, E167.988°) some 5 km to the north, primarily caught blue cod. This indicates that there may be substantial variations in prey composition on small spatial scales.

Video data recorded on four penguins from Boulder Beach in November 2016 showed that the birds sometimes forage in the water column under certain circumstances, rather than using their usual benthic foraging (*https://youtu.be/YkLeB3J8b-Q*). Due to high algal productivity in the water column, visibility at the seafloor (>50m) was close to zero; as a a result, penguins used a pelagic foraging strategy that can be described as "jellyfish harvesting". The penguins sought out jellyfish – mostly crystal jellyfish (*Aequorea forskalea*) but also lion's mane (*Cyanea capillata*) and salp chains (*Salpidae*) – and preyed on commensalistic fish swimming under the jellyfish's bell or close to the salp chain. Prey identification proved difficult from the video data but judging from the apparent length of the fish they may have been juvenile sprat (confirmed in some instances) or red cod. van Heezik (1990a) found that the penguins caught predominantly larval stages of red cod (30mm) in the spring time, when phytoplankton blooms occur (Murphy et al., 2001). Abundance of jellyfish correlates with the phytoplankton blooms (Richardson et al., 2009), so that it is plausible that red cod larvae may indeed be associated with jellyfish. Another instance of "jellyfish harvesting" was observed during a camera deployment on a penguin from Hinahina Cove in the Catlins in December 2017 (Mattern et al., unpublished data).

Another successful camera deployment in December 2017 on a bird from Penguin Bay, Catlins, showed that the bird foraged on the seafloor at depths of close to 120m (*https://youtu.be/6KTqntfbo1A?t=1m34s*). There was a noticeable behavioural difference when compared to benthic foraging penguins from the Otago Peninsula in that the Catlins bird always swam at high speed while at the seafloor, suggesting that benthic foraging at these depths requires higher swimming speeds to cover more ground in the short period available at the bottom and is, thus, likely more energy demanding. However, further data is required to assess whether this is true for deep-diving Yellow-eyed penguins penguin in general.

Prey sizes, age classes & temporal occurrence

Yellow-eyed penguins tend to forage for relatively small-sized prey ranging between 50-150 mm; the exception being blue cod which was found in all studies to range in length between 150 and 220 mm (Figure 4). The prey sizes allow some conclusions to be drawn about the life stages of prey that are taken by Yellow-eyed penguins (Table 1). The penguins target primarily larval and juvenile stages, except for small species like ahuru, sprat and silverside, which are also taken as adults.

van Heezik (1990a) and Moore & Wakelin (1997) found that the length of some prey species varied with the time of the year. For example, ahuru prey were principally juveniles in the summer, but adults were taken in autumn and winter (Moore & Wakelin,1997); van Heezik (1990a) recorded ahuru only in the winter, the majority of which were adults. The situation was less clear for silverside, since Moore & Wakelin (1997) found that various age-classes were taken in winter, while juveniles dominated in spring through to summer (Moore & Wakelin,1997). Yet, van Heezik (1990a) found all age-classes of silversides in autumn, mainly juveniles in winter and spring, and predominantly adults in summer.

van Heezik (1990b) provides some data indicating that young juvenile squid (dorsal mantle length: mean 14 mm, median: 5 mm, range: 5-55 mm) were targeted. Similarly, the mean mass of arrow squid was 55g, with small (<20g) squid taken at all times, but larger squid (20-240g) more often taken in January-February (Moore & Wakelin, 1997). Juvenile arrow squid are known to occur predominantly in the upper 100 m of the water column (Mattlin, Scheibling & Förch, 1985).

Table 1. Sizes and age classes of the main prey species taken by Yellow-eyed penguins from the New Zealand mainland. Adult fish length data was derived from species queries at fishbase.org except where an alternative citation is provided. Superscript numbers indicate data sources for the calculation of mean prey lengths taken by the penguins.

Prey species	Common adult length	Mean length taken	Prey life stage
Sprat	90 mm	66 ± 1 mm[1,2]	juvenile-adult
Red cod	50 mm	65 ± 8 mm[1,2]	larval
Ahuru	100 mm	100 ± 6 mm[1,2]	juvenile-adult
Silverside	250 mm	120 ± 7 mm[1,2]	larval-adult
Opalfish	280 mm (max length)	131 ± 14 mm[1,2,3,4]	juvenile
Blue cod	350 mm	186 ± 28 mm[2,3,4]	juvenile
Arrow squid	260 mm (Smith et al., 1987)	14 mm[3]	juvenile

[1]van Heezik 199a, [2]Moore & Wakelin 1997, [3]van Heezik 1990b, [4]Browne et al. 2011

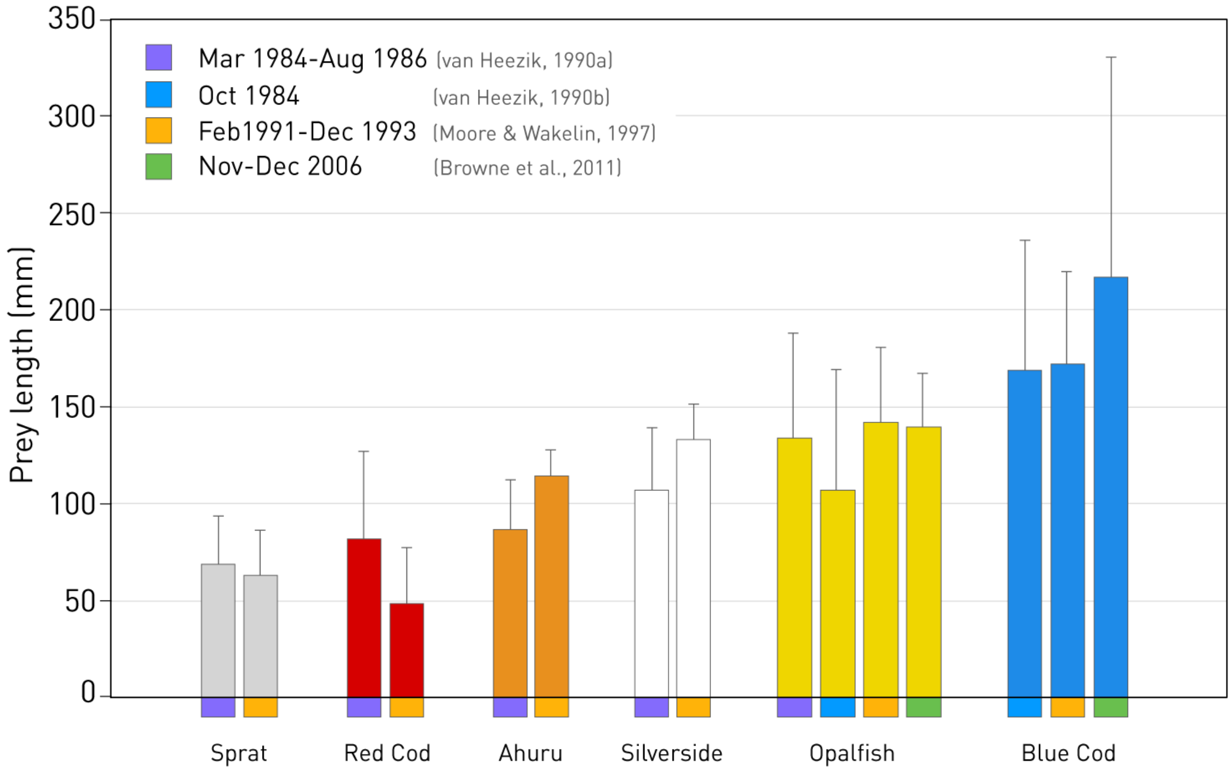

Figure 4. Mean prey sizes (plus standard deviation) determined during the four main diet studies conducted on Yellow-eyed penguins since the mid-1980s.

Differences between adult & juvenile penguins

The only information about the differences in the diet of adult and juvenile Yellow-eyed penguins is reported by van Heezik (1990a,b). When comparing 82 juveniles with 512 adults sampled across their mainland distributional range (van Heezik, 1990a), it appears as if juveniles tend to target prey species that generally occur in schools, especially arrow squid (Norman & Reid, 2000) and sprat. This may also apply to red cod, which as an adult is a principally benthic species, but occurs pelagically during its early life stages (Habib, 1973).

These data suggest that juvenile Yellow-eyed penguins may forage to a greater extent pelagically than adults (e.g. Mattern et al., 2007, 2013), although opalfish and ahuru, which are demersal species (Paulin et al., 2001), were also caught by juveniles (van Heezik, 1990a).

Prey behaviour & capture strategies

Apart from stock assessment studies, there is surprisingly little information about the behavioural ecology of fish species in New Zealand, particularly larval and juvenile stages, and non-commercial species in general. Consequently, it is difficult to put the Yellow-eyed penguins' prey composition into an ecological context. Some inferences can be made from the penguin diet studies, such as the potential association of red cod larvae with jellyfish (see above). Recent deployments of animal-borne cameras provide new insights into the predator-prey relationship between Yellow-eyed penguins and their main target species.

With regard to the main demersal species caught by Yellow-eyed penguins, there is a clear difference in prey behaviour that is of relevance to the penguins.

Opalfish tend to rely on camouflage as a method of predator evasion. Caught mainly over sandy or gravelly sediment, opalfish blend in with the environment. If an opalfish is located, there is generally no pursuit involved: penguins hover over the fish until they have extracted it from the sediment, and then it is always ingested at the seafloor (*https://vimeo.com/269344700*). This means that multiple captures of opalfish can occur during single dives.

In contrast, blue cod are almost always captured after prolonged pursuits which requires considerably higher energy investment by the penguin when compared with catching opalfish. Moreover, due to the large size of blue cod, the ingestion can take up to a minute or two and often involves the penguin swimming to the surface with its prey (*https://vimeo.com/269345029*). Additionally, blue cod pursuits do not always end in successful prey capture. Nevertheless, the energetic payback for the adults is likely greater when catching single large prey, compared to multiple small prey.

Off the Otago Peninsula, captures of sprat generally occur from below the targeted individual (*https://vimeo.com/269344737*). Sprat are clearly visible against the light backdrop of the sea surface and often caught without the fish showing any obvious reaction to the penguins' presence. Sprat associated with jellyfish generally try to flee but are generally captured after brief pursuit. Interestingly, sprat were generally seen in the videos as individuals; schools were not recorded although Yellow-eyed penguins preying on schools of baitfish has been observed on the Auckland Islands (*https://vimeo.com/269344737#t=1m06s*). On Stewart Island, juvenile tarakihi are generally captured close to the seafloor, mainly over sandy bottoms after brief pursuits; ingestion occurs at the sea floor (*https://vimeo.com/269344610*).

Prey association with benthic sediments

The sedimentary composition determines what prey species are caught by Yellow-eyed penguins (Mattern et al., 2017a). While a detailed analysis of the prey association with different seafloor types from video data is still pending, some general conclusions can be drawn.

Opalfish, sprat, and juvenile tarakihi are species principally caught over finer sediments, i.e. sandy bottom or gravel (Figure 5a & b). Blue cod are more often in regions with greater structural variation, such as coarse gravel and horse mussel fields, as well as oyster beds off Stewart Island (Figure 5c). Jock stewart occur associated low reef structures outside of Golden Beach, Stewart Island (Figure 5d).

Figure 5a. Capture of an opalfish off the Otago Peninsula over coarse sandy bottom with noticeable sediment ripples, a habitat which opalfish captures were particularly common.

Figure 5b. Capture of a juvenile tarakihi over fine sand off Murray Beach, north-east Stewart Island.

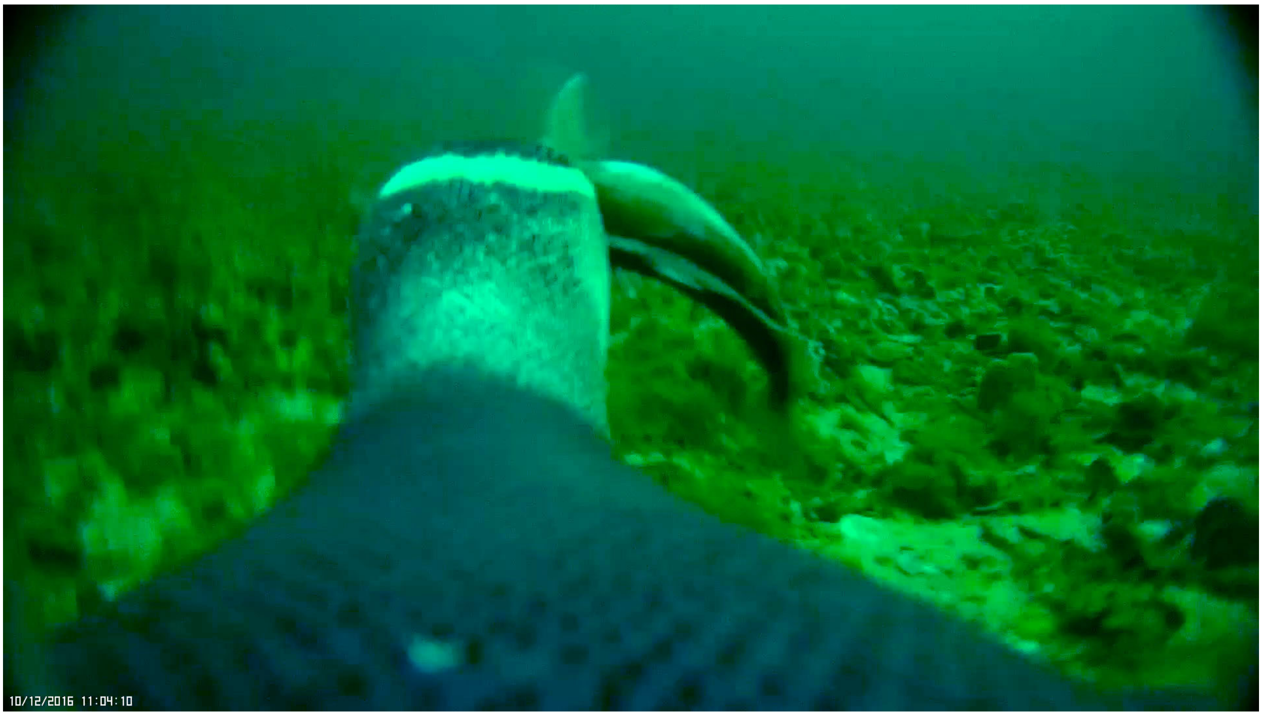

Figure 5c. Capture of a blue cod over highly structured seafloor habitat off Saddle Point, north-east Stewart Island.

Figure 5d. Yellow-eyed penguin capturing a jock stewart over a shallow reef off Golden Beach, Stewart Island. The bird fitted with camera had pursued the fish for about 20 seconds when the second penguin swooped in to steal the catch.

Indirect fisheries effects on prey composition and behaviour

While the direct effects of fisheries on Yellow-eyed penguins, particularly bycatch in set nets, have been apparent since the 1980s (Darby & Dawson, 2000; Ellenberg & Mattern, 2012; Trathan et al., 2015; Crawford et al., 2017), potential indirect effects were first noted in the mid-2000s.

Linear foraging along bottom trawl furrows

During the breeding season 2004/05, Yellow-eyed penguins from Boulder Beach, Otago Peninsula tracked with GPS dive loggers exhibited extraordinary linear foraging movements. Birds swam along straight line courses for several kilometres, sometimes backtracking along the same path (Mattern et al., 2013). Similar foraging patterns were apparent again in 2012/13. It was suspected that the birds used trawl marks on the seafloor for orientation which was investigated with a remote operated vehicle (Mattern et al., 2013). The study found clearly visible, straight furrows that matched the trajectory of the penguins' movements. Judging by the size and length of the furrows, the authors surmised that they were created by otter boards from bottom trawls. An increased presence of blue cod thought to be scavenging in the wake of the fisheries' seafloor disturbance was considered a likely explanation why penguins follow trawl marks (Figure 6). The authors argued that, in essence, the penguins were exploiting a predictable prey source (Mattern et al., 2013).

Foraging habitat changes as a result of oyster fisheries

A comparative study of the foraging movements of Yellow-eyed penguins breeding on Stewart Island/Rakiura and Codfish Island/Whenua Hou found significant differences in foraging ranges between the sites (Mattern, Ellenberg & Davis, 2007). Penguins nesting along the Northeast coast (Anglem coast) of Stewart Island exhibited short foraging ranges (mean: 11.7 ± 4.8 km, n = 13) and often returned after just a few hours at sea, while birds from Codfish Island travelled much greater distances (foraging range: 55 ± 6.2 km, n = 17 birds), sometimes performing overnight trips (Ellenberg & Mattern, 2012). This was an unexpected pattern as, at the time, breeding success on Stewart Island was much poorer than on Codfish Island with starvation being an important cause of chick mortality (King, 2008). Penguins are generally believed to respond to poor foraging conditions by

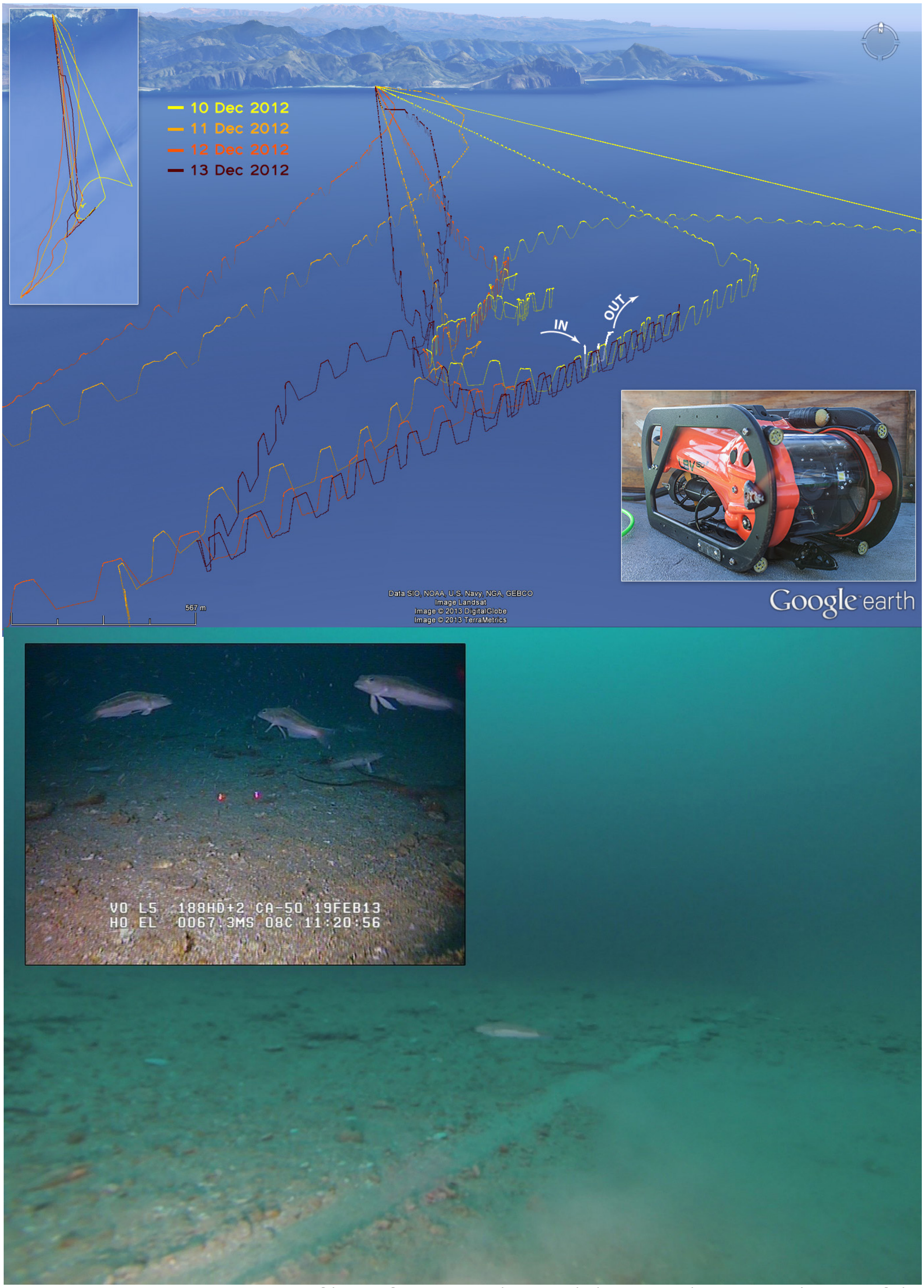

Figure 6. *Top:* 3D representations of linear foraging tracks recorded in December 2012 and image of the ROV used to survey seafloor; white arrows indicate deployment site of ROV. *Bottom:* Highly visible furrow running in a straight line along the seafloor. Inset shows detail of blue cod in pursuit of ROV; scaling lasers represent 5 cm. See also *http://vimeo.com/64689982* (reproduced from Mattern et al., 2013).

extending their foraging ranges (Davis & Renner, 2003). At the same time, blue cod was the single most important prey species on Stewart Island. Browne et al. (2011) argued that the poor breeding success could be explained by the 'junk food hypothesis' in that adult penguins were obtaining prey that was unsuitable for their chicks. In this case, the blue cod brought ashore was too big for small chicks to swallow (Browne et al., 2011).

Limited foraging ranges and quasi mono-specific diet suggest the foraging habitat of the penguins has become limited as a result of the effects of oyster fishery (Ellenberg & Mattern, 2012). The oyster fishery in Foveaux Strait has significantly reduced benthic biodiversity in the region (e.g. Cranfield, Michael & Doonan, 1999; Cranfield et al., 2001; Jiang & Carbines, 2002; Carbines, Jiang & Beentjes, 2004). Furthermore, penguins from Stewart Island foraged mainly outside of the management zones of the oyster fishery, which resulted in principally near-coast movements (Mattern, Ellenberg & Davis, 2007).

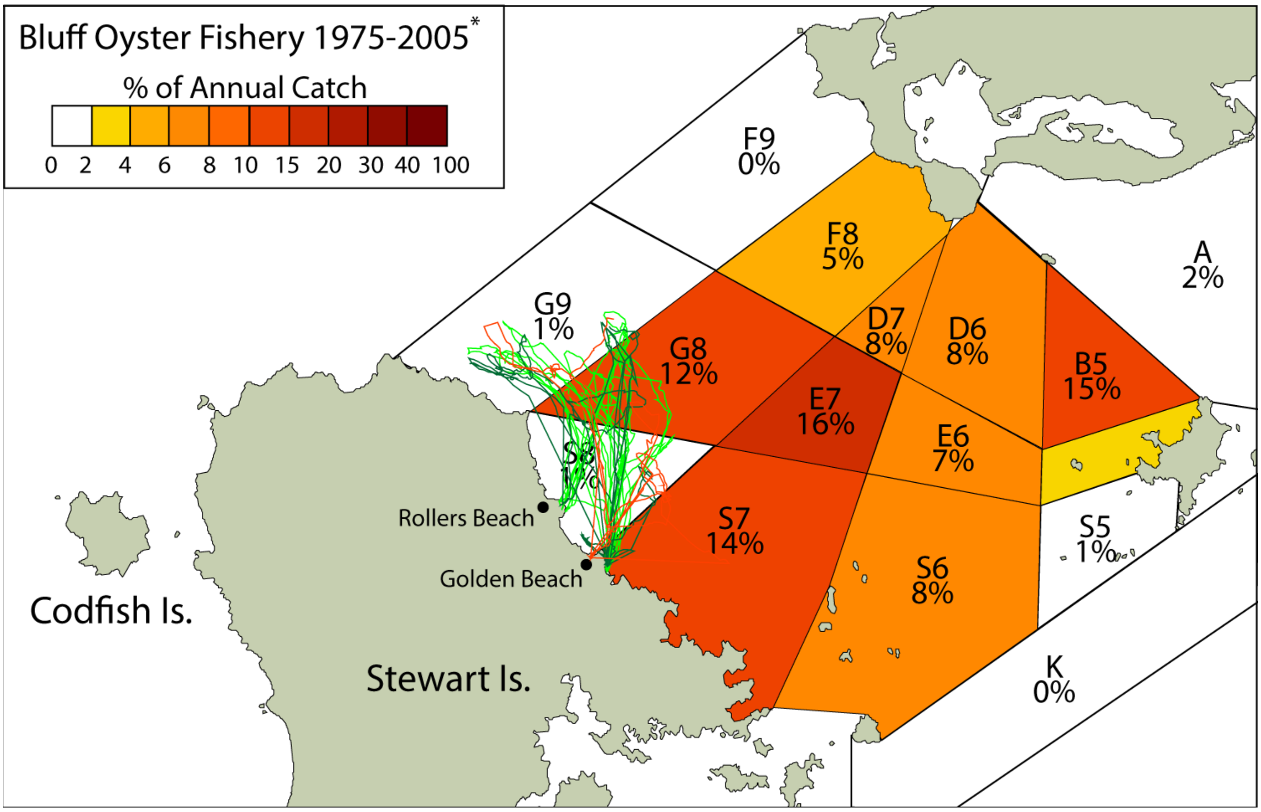

Figure 7. Foraging movements of Yellow-eyed penguins from Stewart Island in relation to the oyster fishery's effort in Foveaux Strait. Fishing effort is given as % of the average annual catch as published in the Appendix II of the Ministry of Fisheries' November 2006 Foveaux Strait Dredge Oyster Fisheries Plan (*http://www.eudyptes.net/?mdocs-file=68*)

Discussion

From the quantitative Yellow-eyed penguin diet data it appears as if the species has seen some considerable changes in their main prey composition since the 1980s, not only with regard to prey species taken but, perhaps more crucially for reproductive success and subsequently population developments, also in prey size with larger prey in recent years. While it is likely that such changes are the result of a combination of multiple factors (Mattern et al., 2017b), there are clear indications that impacts from fisheries have had a significant effects on Yellow-eyed penguin prey composition and foraging behaviour.

The decline of red cod as an important prey species

One of the most striking changes in Yellow-eyed penguin diet composition is the apparent gradual decline in the importance of red cod as a main prey species in some regions since the 1980s (Figures 1-3).

Red cod are a fast-growing, short lived, demersal fish species which is known to undergo significant population fluctuations due to varied recruitment (Ministry of Primary Industries, 2017). The abundance of red cod correlates with ocean temperatures in that good recruitment (and subsequently increased stock) is observed in years of lower sea surface temperatures (Beentjes & Renwick, 2001). Average sea surface temperatures off the south-east coast of the South Island have steadily increased since the mid-1990s, which likely had an effect on red cod abundance in the past two decades. At the same time, commercial landings of red cod declined substantially in management zone RCO3, which encompasses the Yellow-eyed penguins' mainland distribution (Figure 8). The length and magnitude of the declines suggest that fishing pressure may have contributed to a reduction in spawning stock abundance (NZ Ministry of Fisheries, 2007). In response, the total allowable catch was reduced by 63% from October 2007 onwards. The stock then briefly resurged around 2012, but has since dropped again to 2007 levels (Ministry of Primary Industries, 2017). It appears as if a combination of increasing ocean temperature from the mid-1990s and fishing pressure until the mid-2000s has resulted in a reduction in red cod abundance, likely making this species a less viable prey source for Yellow-eyed penguins today.

Red cod contributed considerably more biomass to the Yellow-eyed penguins' diet in the mid-1980s (van Heezik, 1990a) when compared to the early 1990s (Moore & Wakelin, 1997) (Figure 3). Reported commercial landings of red cod (Ministry of Primary Industries, 2017) provide an indication of its availability as prey to Yellow-eyed penguins. Red cod landings seem to have been only marginally lower while Moore & Wakelin (1997) were conducting their study compared to landings reported when van Heezik (1990a) was researching penguin diet (Figure 7). So why did the penguins take less red cod in the 1990s?

A likely explanation for the lower biomass intake of red cod by Yellow-eyed penguins in the 1990s could be that recruitment of red cod had declined since the mid-1980s, meaning fewer red cod of the size class targeted by the penguins were available. Considering that ocean temperatures experienced a lower-than-average period in between 1991 and 1996 (Mattern et al., 2017b), this apparent lack of red cod recruitment would seem at least partly attributable to fishing pressure (NZ Ministry of Fisheries, 2007).

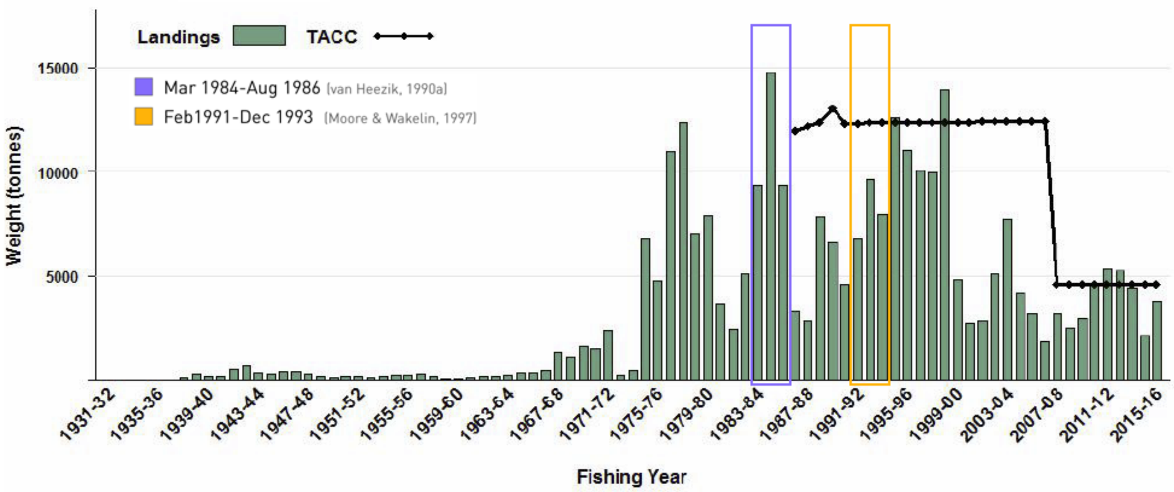

Figure 8. Reported commercial catch of Red Cod in management zone RCO3 (south-eastern New Zealand) and the time period during which the two major penguin diet studies were conducted. Graph adapted from (Ministry of Primary Industries, 2017)

The rise of blue cod as a main prey species

At the same rate as red cod disappeared from the Yellow-eyed penguins' diet, blue cod increased in importance as a prey species (Figs 1-3), which holds true today as recent camera deployments on Yellow-eyed penguins from the Otago Peninsula have demonstrated (Mattern et al., 2017a; Mattern et al. unpublished data).

Blue cod are a bottom-dwelling, long-lived fish species endemic to New Zealand (Paulin et al., 2001; Ministry of Primary Industries, 2016). It has been described as a 'voracious feeder' that predominantly feeds on crustaceans, fish and molluscs (Graham, 1939). In terms of its benthic habitat, blue cod is a versatile and hardy species that can exist on disturbed, fished seafloor habitat as well as on undisturbed intact areas of high benthic biodiversity (Jiang & Carbines, 2002).

Bottom fisheries generally have detrimental effects on the complexity of benthic communities and are a major cause of reduced seafloor biodiversity (e.g. Turner et al., 1999; Thrush & Dayton, 2002; Bradshaw, Collins & Brand, 2003; Hinz, Prieto & Kaiser, 2009). With the slow recovery of benthic habitats after fishing disturbance (e.g. Cranfield et al., 2003) even single bottom-fishing events can have long lasting effects on local biodiversity. Therefore it is reasonable to assume that bottom fisheries inevitably will have a cascading effect on Yellow-eyed penguins through a reduction in prey diversity and abundance (Browne et al., 2011; Ellenberg & Mattern, 2012; Mattern et al., 2013).

The removal of epibenthic structures (e.g. horse mussels, sponges, ascidians etc.) in the wake of bottom fisheries also leaves smaller marine animals exposed to the elements and predators which eventually leads to the disappearance of these smaller species (Kaiser & Spencer, 1994). The effect of benthic fishing on Yellow-eyed penguins may be two-fold. While, on the one hand, scavenging and hardy fish species such as blue cod may be more readily available (Mattern et al., 2013) (Figure 6), these species may, on the other hand, be less optimal prey than smaller species, especially when feeding small chicks.

Blue cod is the largest prey species taken by Yellow-eyed penguins (Figure 4). Given that it is more frequently caught (Figure 2) and contributes more to the relative prey biomass since the 1990s (Figure 3) it can be considered a staple food item for adult Yellow-eyed penguins. However, despite its adequate nutritional value, blue cod may not be suitable food for chicks (Browne et al., 2011). Compared to slender-bodied opalfish, blue cod are

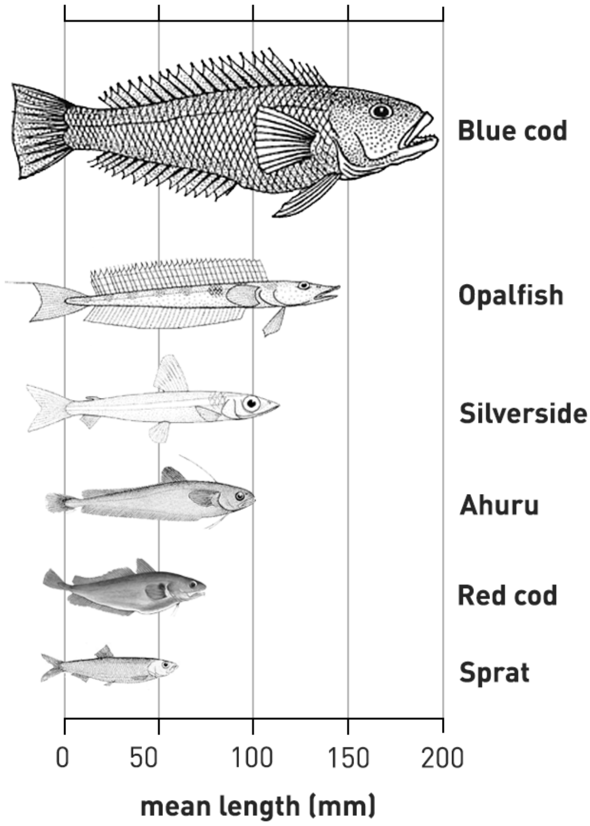

Figure 9. Comparison of approximate lengths and body shapes of main prey species as recorded in Yellow-eyed penguin diet.

Figure 10. Two hardly digested blue cod found close to a Yellow-eyed penguin chick about to fledge in Sealers Bay, Whenua Hou/Codfish Island, 28. February 2018. Both fish were between 210 and 250 mm long.

very muscular, stocky fish (Paulin et al., 2001; Figure 9) that presumably take longer to digest and break down into smaller parts, resulting in over-sized fish being transfered to chicks (Wilson et al., 1985). Spills of hardly digested blue cod at nest sites with underweight chicks may support this hypothesis (Figure 10). However, similar food spills have been observed since the early 1990s (Chris Lalas, pers. comm.); whether these spills are more common today – or are indeed associated with lower chick weights or starvation – requires additional investigation.

Further evidence comes from underwater video. Some adult Yellow-eyed penguins that were equipped with cameras during the chick rearing period opted not to pursue blue cod when the chance arose, probably searching for smaller prey (*https://vimeo.com/269344577*). There may also be a trade-off between the extra effort needed to capture and handle blue cod, along with the risk of failing to catch the prey, compared with the relative ease of capturing smaller prey.

Another question the size of blue cod raises, is why the penguins do not go after smaller specimen to start with. Especially on fished grounds, blue cod tend to be smaller than over undisturbed habitat (Carbines, Jiang & Beentjes, 2004). One possible explanation could be that given blue cod's tendency to flee, the energy required to capture this species makes the pursuit of smaller specimen unviable for the penguins. This would also offer an explanation why blue cod was also the largest species caught historically (Figure 4)

Regional benefits of opalfish abundance

Along with red cod and blue cod, opalfish has been a very important prey species in terms of biomass in Yellow-eyed penguin diet (Figure 4). However, there are substantial regional differences. At least in the 1980s, opalfish were the predominant prey species at Moeraki, Boulder Beach/Otago Peninsula, Long Point/Catlins and Codfish Island/Whenua Hou. What these sites have in common is accessibility of coarse sand/moderate gravel sediments (Figure 1), which, judging from video footage (Figure 5a), is the preferred habitat of opalfish (Mattern et al., 2017a). The species' reliance on camouflage to blend in with the variable colouration of coarser sediments, may explain why it is of lesser importance in areas dominated by fine sediments (e.g. northern Catlins, regions North of Otago Peninsula, Figure 1).

Opalfish represent an ideal food source for Yellow-eyed penguins. Firstly, it is not a commercial species, so fisheries interactions are unlikely to have direct effects on its ecology. Secondly, it appears to be an easy prey to catch as the penguins generally capture them without the need for energy-consuming prey pursuits (Mattern et al., 2017a). Thirdly, compared to other prey, opalfish provide the highest energy (opalfish 8.5 ± 1.9 kJ g^{-1}, red cod: 7.3 ± 0.5 kJ g^{-1}, arrow squid: 6.3±0.6 kJ g^{-1}, blue cod: 5.95 kJ g^{-1}) and crude protein contents (opalfish: 30.3 ± 6.3% of wet mass, blue cod: 19.9%, red cod: 18.0 ± 1.0%, arrow squid: 18.9 ± 1.2%) (Meynier et al., 2008; Talley's Group Limited, 2018). Its smaller size compared to blue cod means that more opalfish have to be caught to acquire the same amount of prey biomass. However, preliminary prey encounter rates suggest that where it is available, opalfish is more commonly caught than blue cod (Mattern et al., 2017a).

The relevance of pelagic species – sprat and arrow squid

Besides red cod, blue cod and opalfish – all of which are benthic species – Yellow-eyed penguin also were found to prey on pelagic species, most notably slender sprat and arrow squid. In terms of their frequency of occurrence both species ranked as high as red cod in the 1980s and blue cod in the 1990s (Figure 3). Yet, in terms of mass contribution both species hardly exceeded more than 20% to the penguins' diet (Figure 4), so that they can be considered important, but not staple prey species.

Slender sprat is of little to no commercial interest in New Zealand (*http://www.nabis.govt.nz/map.aspx?thematic=Commercial%20Catch%20(kg)%20for%20Slender%20sprat*), which may explain why there is hardly any published information on species abundance or ecology. In fact, most scientific publications that mention slender sprat revolve around their role as prey for marine vertebrates (e.g. Childerhouse, Dix & Gales, 2001; Fraser & Lalas, 2004; Markowitz et al., 2004). This makes it difficult to understand why sprat appeared to become less important in the penguins' diet between the 1980s and 1990s. One possible explanation, however, could be that the capture of sprat is predominantly an opportunistic occurrence, i.e. the penguins capture sprat when they encounter them, but have not specifically adopted a foraging strategy for it.

When foraging at the seafloor, sprat encounters are a rare occurrence (Mattern et al., 2017a; Mattern et al., unpublished data). Instead the penguins tended to capture the clupeids either during encounters while ascending back to the surface from the seafloor or when oceanic conditions forced the penguins to abandon benthic foraging. Interestingly, the observed sprat captures were of single individuals. Yet, slender sprat is known to occur in large schools that a Yellow-eyed penguin will likely exploit if encountered.

The predominantly benthic foraging strategy of Yellow-eyed penguins where the birds search for prey along the seafloor may reduce their chances to encounter schools of sprat in the water column. But at the same time, this strategy has been described as a potential mechanism to reduce competition with other seabirds while the seafloor provides a stable, predictable source of benthic prey (Mattern et al., 2007). Hence, in years of increased sprat abundance, the clupeid may feature more prominently in the penguins' diet, but the penguins' foraging habits do not suggest that they are as important as benthic prey.

As with sprats, the abundance of arrow squid in the penguins' diet is likely dictated by the same opportunistic mechanisms that come with the penguins' benthic foraging habits. However, unlike sprat there is a considerable arrow squid fishery within most of the Yellow-eyed penguin's breeding range (*https://bit.ly/2KZO0eK*). This means that the abundance and availability of arrow squid for the penguins may be influenced by fishing activities. Yet, while arrow squid often appeared in penguin stomachs in all studies (Figure 1), the species' biomass contribution to the penguins' diet is not significant (Figure 3). Moreover, the lower overall nutritional value (see above) and the small size of the arrow squid generally taken (Figure 4) probably renders them a less preferred species to the penguins.

Potential indirect fisheries impacts

While direct fisheries impacts, most notably bycatch in set nets, have been identified in the past decades (e.g. Darby & Dawson, 2000; Ellenberg & Mattern, 2012; Crawford et al., 2017), indirect effects are far more difficult to ascertain. Resource depletion as a result of fisheries competition is believed to be an issue for pelagic foraging penguin species in some regions (Trathan et al., 2015), and the benthic foraging strategy of Yellow-eyed penguins from the New Zealand mainland makes them particularly susceptible to alteration of the seafloor as a result of fishing activities (Ellenberg & Mattern, 2012). Foraging movements (Figure 7) and diet composition (Browne et al., 2011) of penguins breeding on Stewart Island provide some evidence for the potential effects of bottom fisheries-related disturbance of benthic habitats.

Oyster fishery in Foveaux Strait

The Bluff oyster fishery has been active for more than 130 years (Cranfield, Michael & Doonan, 1999), so that it can be argued that any negative effects on Yellow-eyed penguin foraging habitat should have made an impact on the species a long time ago. However, the fishery has intensified significantly since the 1960s. Many oyster beds that were traditionally located in the eastern Foveaux Strait became commercially unviable, during the 1980s, with the result that the fishery moved westwards and overlapped with the Yellow-eyed penguin foraging grounds off the Anglem coast (Cranfield, Michael & Doonan, 1999). An outbreak of the epizootic *Bonamia exitosa* caused major mortality in the oyster population which disrupted the fishery between 1986 and 1991, followed by complete closure between 1992 and 1995 before the fishery resumed again (Yang, Frazer & Rees, 2010).

As such, it is plausible that Yellow-eyed penguins experienced low exposure to major fisheries until after the Bonamia outbreak, so that the oyster fishery only impacted on the penguins since the mid-1990s. Unfortunately, robust Yellow-eyed penguin population data is not available for the early periods (see Darby, 2003), but a decline in Yellow-eyed penguin numbers along the Anglem coast was recorded between 1999 and 2008 (King et al., 2012). However, whether this is an example of indirect fisheries effects remains a matter of conjecture.

Bottom trawling off the mainland coast

Assessing the impact of bottom trawling on Yellow-eyed penguin foraging habitat is even more difficult. There is a major body of scientific publications that document the negative effects of bottom trawling on epibenthic communities and subsequently benthic biodiversity (e.g. Schratzberger & Jennings, 2002; Lokkeborg, 2005; Queirós et al., 2006; Hinz, Prieto & Kaiser, 2009). However, measuring the impact of benthic disturbance on Yellow-eyed penguin foraging success is impossible due to a lack of knowledge about historical data on benthic biodiversity, data on regenerative processes of the distinct benthic biomes used by Yellow-eyed penguins for foraging, as well as reliable and accessible fisheries data. This is illustrated well using the example of the Otago Peninsula.

According to data collated by the South-East Marine Protection forum (see *https://www.seasketch.org/#projecthomepage/5331eff529d8f11a2ed3dd04*), the sea floor areas where Yellow-eyed penguins from Boulder Beach mainly forage have little to no trawl activity. Yet, surveys of the sea floor off the Otago Peninsula in February 2013 found evidence of trawling including long parallel furrows matching the dimensions of trawler otter boards, along with smashed bivalve shell fragments, the presence of scavenging species and the general lack of epibenthic, sessile fauna (Figure 6; Mattern et al., 2013). The foraging behaviour of Yellow-eyed penguins was altered significantly depending on whether the birds foraged over intact or fished seafloor, with penguins showing much more randomised movements over the former and linear trajectories following trawl marks over the latter (Mattern et al., 2013). It is unclear whether these different behaviours were reflected also in the type of prey they brought ashore, although the authors argue that blue cod may have dominated the diet in penguins that foraged over fished habitat. The potentially negative consequences for reproductive success of penguins employing such a strategy are discussed above.

Beyond fisheries impacts – sedimentation and pollution

There are other factors that influence the state of the sea floor habitat. It has long been argued that agriculture increases the sediment influx into coastal ocean systems (e.g. Walling, 2006). Whereas agricultural practices themselves may not necessarily increase transport of sediments into the ocean (Griffiths & Glasby, 1985), intensity of rainfall is an important determinant for increased sedimentation (Hicks, Gomez & Trustrum, 2000). With climate change models predicting a reduction of rainfall along the South Island's east-coast (Mullan, Wratt & Renwick, 2002), the problem of near-shore sedimentation may actually lessen. On the other hand, the intensification of dairy farming in New Zealand has greatly reduced water quality of many major rivers. While the environmental impacts of these farming trends are hotly debated (e.g. Foote, Joy & Death, 2015; Larned et al., 2016), there is surprisingly little information available on the effects of influx of polluted waters into the coastal ecosystems. Unsurprisingly, it is impossible to gauge how much Yellow-eyed penguins are affected pollution in the marine habitat.

Conclusion/recommendations

Any human activity that degrades the Yellow-eyed penguin's benthic habitat will inevitably affect their foraging behaviour, and ultimately the success of the species itself. However, the degree to which fisheries indirectly affect Yellow-eyed penguins remains poorly understood.

Perhaps understandably, most conservation and monitoring efforts for Yellow-eyed penguins have focused on the terrestrial environment. These efforts began in the 1930s (Moore 2001), and have been almost continuous in some parts of the mainland range since the early 1980s (Darby, 1985; Efford, Spencer & Darby, 1996; Ellenberg & Mattern, 2012). Clearly, introduced predators, human disturbance and destruction of breeding habitat have had major impacts on Yellow-eyed penguins and these factors needed to be addressed. However, starvation events and population declines have shown that the marine environment also has a major part to play in population dynamics (Gill & Darby 1993, Moore & Wakelin 1997).

Despite this, studies of how Yellow-eyed penguins interact with the marine environment have been sporadic since the 1980s (Seddon & van Heezik, 1990; Moore, 1999). More recent studies in the last 15 years (Mattern et al., 2007, 2013; Ellenberg & Mattern, 2012; Chilvers, Dobbins & Edmonds, 2014; Melanie Young, unpublished data), provide only snapshots of the species' foraging behaviour and prey composition. However, a more thorough understanding of the penguins' marine ecology is crucial if we want to understand what drives population numbers. With tracking technologies becoming smaller, cheaper and easier to handle, and the advent of new ways to determine what penguins consume, it is high time to include the marine aspect of their biology in conservation management of Yellow-eyed penguins. Only then will it be possible to reliably assess direct and indirect effects of anthropogenic influences on our most endangered penguin species.

Following is a list of recommendations to expand the monitoring programmes in an effort to better understand the Yellow-eyed penguins' marine ecology.

1. **Use GPS dive trackers at representative sites on an annual basis to detect any changes in foraging ranges in relation to anthropogenic activities.**

   Single deployments (5-7 days) on 10-20 birds during the breeding and non-breeding season every year, each in North Otago, Otago Peninsula, Catlins & Stewart/Codfish Island. This will result in 60-100 tracks per year and site which suffices to calculate habitat kernels and determine where penguins foraging overlaps with human activities. Recommended devices: MobileAction i-gotU GT-600 GPS loggers combined with TechnoSmArt AxyDepth TDRs. All devices are re-deployable. A regular foraging monitoring programme will provide continuous timeseries data of foraging parameters (similar to population monitoring data) that can then be modelled against environmental factors and fisheries activities to gain a better understanding of how these factors determine the penguins' at-sea behaviour, foraging success and reproductive output.

2. **Establish a non-invasive diet monitoring programme.**

   This is best achieved using either DNA analysis of faecal samples and deployment of animal-borne cameras conducted in tandem with tracking recommended above. Establishing the diet composition of the penguins is vital to understand how foraging behaviour correlates with observed demographic parameters (e.g. reproductive success, survival). Correlating DNA signals in faeces with observations from video loggers will cover both the quantitative (e.g. frequency of occurrence of prey types from DNA) and qualitative aspects (e.g. prey capture rates, prey sizes) required for a comprehensive understanding of the penguins' dietary preferences. Besides reducing impact of research on the birds' well-being, the advantage of this approach is that analysis is far less labour-intensive compared to stomach flushing and can be conducted by a wider range of observers and, thus, be conducted on a broader scale.

   Although a recent publication (Goldsworthy et al., 2016) has found no negative effects of stomach flushing in Yellow-eyed penguins, it has to be kept in mind that the majority of the data available for this study originated from the studies by van Heezik (1990a,b) and Moore & Wakelin (1997), i.e. during a period when Yellow-eyed penguins consumed smaller prey items than today. Particularly, flushing penguins that hold large blue cod specimen in their stomachs poses a substantial risk due to the sharp spines in the blue cod's dorsal fins. Forcing regurgitation of such specimen has resulted in one confirmed Yellow-eyed penguin death as a result of oesophageal laceration and internal bleeding on Codfish Island (Mattern, personal observation). Therefore, as long as blue cod is suspected to be a major component of the penguins' diet, stomach flushing Yellow-eyed penguins is not advised.

3. **Regular collection of feathers and blood samples for current and future stable isotope analyses.**

Feather clippings should be collected from every handled bird to build a feather library that can be used to determine trends in the trophic levels of consumed prey as has been done in other New Zealand penguin species (e.g. Hilton et al., 2006; Mattern et al., 2009). Blood samples integrate prey composition over the course of a few weeks and, thus, provide a more immediate take on the penguins diet intake (e.g. Flemming & van Heezik, 2014).

4. **Conduct a comprehensive baseline study of Yellow-eyed penguin foraging ecology on the sub-Antarctic Islands.**

Our knowledge about Yellow-eyed penguin ecology in the sub-Antarctic is poor. Despite this, these populations are frequently cited as 'insurance' populations if the penguins continue to disappear from the New Zealand mainland. Without any baseline information it will be very difficult to determine factors behind any future population changes on Auckland and Campbell Islands. The latter island should be of particular interest as the surrounding bathymetry does not seem conducive to the penguins' predominantly benthic foraging strategy observed on the mainland. Hence, the Campbell Island population can provide some crucial information about the species' flexibility in a more dynamic, pelagic marine environment.

Acknowledgments

This report is funded by the Department of Conservation's Conservation Services Programme. Special thanks are due to Peter Moore, Yolanda van Heezik, John Darby, Bruce McKinlay and Chris Lalas for reviewing and commenting on early drafts of this document and for sharing personal insights not found in published materials.

References

Beentjes MP., Renwick JA. 2001. The relationship between red cod, *Pseudophycis bachus*, recruitment and environmental variables in New Zealand. Environmental Biology of Fishes 61:315–328. DOI: 10.1023/A:1010943906264.

Boyd PW. 2011. Beyond ocean acidification. Nature Geoscience 4:273–274. DOI: 10.1038/ngeo1150.

Bradshaw C., Collins P., Brand AR. 2003. To what extent does upright sessile epifauna affect benthic biodiversity and community composition? Marine Biology 143:783–791. DOI: 10.1007/s00227-003-1115-7.

Browne T., Lalas C., Mattern T., Van Heezik Y. 2011. Chick starvation in yellow-eyed penguins: Evidence for poor diet quality and selective provisioning of chicks from conventional diet analysis and stable isotopes. Austral Ecology 36:99–108. DOI: 10.1111/j.1442-9993.2010.02125.x.

Carbines G., Jiang W., Beentjes MP. 2004. The impact of oyster dredging on the growth of blue cod, *Parapercis colias*, in Foveaux Strait, New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 14:491–504. DOI: 10.1002/aqc.608.

Childerhouse S., Dix B., Gales N. 2001. Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. Wildlife Research 28:291. DOI: 10.1071/WR00063.

Chilvers B., Dobbins M., Edmonds H. 2014. Diving behaviour of yellow-eyed penguins, Port Pegasus/Pikihatiti, Stewart Island/Rakiura, New Zealand. New Zealand Journal of Zoology 41:161–170. DOI: 10.1080/03014223.2014.908931.

Cranfield HJ., Carbines G., Michael KP., Dunn A., Stotter DR., Smith DJ. 2001. Promising signs of regeneration of blue cod and oyster habitat changed by dredging in Foveaux Strait, southern New Zealand. New Zealand Journal of Marine and Freshwater Research 35:897–908. DOI: 10.1080/00288330.2001.9517052.

Cranfield HJ., Rowden AA., Smith DJ., Gordon DP., Michael KP. 2003. Macrofaunal assemblages of benthic habitat of different complexity and the proposition of a model of biogenic reef habitat regeneration in Foveaux Strait, New Zealand. Journal of Sea Research 52:109–125.

Cranfield HJ., Michael KP., Doonan IJ. 1999. Changes in the distribution of epifaunal reefs and oysters during 130 years of dredging for oysters in Foveaux Strait, southern New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 9:461–483. DOI: 10.1002/(SICI)1099-0755(199909/10)9:5<461::AID-AQC353>3.0.CO;2-Z.

Crawford R., Ellenberg U., Frere E., Hagen C., Baird K., Brewin P., Crofts S., Glass J., Mattern T., Pompert J., Ross K., Kemper J., Ludynia K., Sherley RB., Steinfurth A., Suazo CG., Yorio P., Tamini L., Mangel JC., Bugoni L., Jiménez Uzcátegui G., Simeone A., Luna-Jorquera G., Gandini P., Woehler EJ., Pütz K., Dann P., Chiaradia A., Small C. 2017. Tangled and drowned: A global review of penguin bycatch in fisheries. Endangered Species Research 34:2017. DOI: 10.3354/esr00869.

Darby JT. 1985. The great yellow-eyed penguin count. Forest & Bird 16:16–18.

Darby JT. 2003. The yellow-eyed penguin (*Megadyptes antipodes*) on Stewart and Codfish Islands. Notornis 50:148–154.

Darby JT., Dawson SM. 2000. Bycatch of yellow-eyed penguins (*Megadyptes antipodes*) in gillnets in New Zealand waters 1979–1997. Biological Conservation 93:327–332.

Davis LS., Renner M. 2003. Penguins. London: T&AD Poyser.

Deagle BE., Chiaradia A., McInnes J., Jarman SN. 2010. Pyrosequencing faecal DNA to determine diet of little penguins: Is what goes in what comes out? Conservation Genetics 11:2039–2048. DOI: 10.1007/s10592-010-0096-6.

Efford MG., Spencer NJ., Darby JT. 1996. Population studies of Yellow-eyed penguins - 1994-94 progress report. Wellington: Department of Conservation.

Ellenberg U., Mattern T. 2012. Yellow-eyed penguin - review of population information. Wellington, New Zealand. DOI: 10.13140/RG.2.2.21606.83523.

Flemming SA., van Heezik Y. 2014. Stable isotope analysis as a tool to monitor dietary trends in little penguins Eudyptula minor. Austral Ecology 39:656–667. DOI: 10.1111/aec.12128.

Foote KJ., Joy MK., Death RG. 2015. New Zealand Dairy Farming: Milking Our Environment for All Its Worth. Environmental Management 56:709–720. DOI: 10.1007/s00267-015-0517-x.

Fraser MM., Lalas C. 2004. Seasonal variation in the diet of blue penguins (*Eudyptula minor*) at Oamaru, New Zealand. Notornis 51:7–15.

Gales RP. 1987. Validation of the stomach-flushing technique for obtaining stomach contents of Penguins. Ibis 129:335–343. DOI: 10.1111/j.1474-919X.1987.tb03177.x.

Goldsworthy B., Young MJ., Seddon PJ., van Heezik Y. 2016. Stomach flushing does not affect apparent adult survival, chick hatching, or fledging success in yellow-eyed penguins (*Megadyptes antipodes*). Biological Conservation 196:115–123. DOI: 10.1016/j.biocon.2016.02.009.

Graham D. 1939. Food of the fishes of Otago Harbour and adjacent sea. Transactions and Proceedings of the Royal Society of New Zealand 68:421–438.

Griffiths GA., Glasby GP. 1985. Input of river-derived sediment to the New Zealand continental shelf: I. Mass. Estuarine, Coastal and Shelf Science 21:773–787. DOI: 10.1016/0272-7714(85)90072-1.

Habib G. 1973. Aspects of the biology of the red cod (*Pseudophycis bachus*). Ph.D. thesis. University of Canterbury. Christchurch, New Zealand

van Heezik Y. 1990a. Seasonal, geographical, and age-related variations in the diet of the Yellow-eyed Penguin (*Megadyptes antipodes*). New Zealand Journal of Zoology 17:201–212.

van Heezik Y. 1990b. Diets of yellow-eyed, Fiordland crested, and little blue penguins breeding sympatrically on Codfish Island, New Zealand. New Zealand Journal of Zoology 17:543–548.

van Heezik Y., Davis LS. 1990. Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. Ibis 132:354–365.

van Heezik Y., Seddon PJ. 1989. Stomach sampling in the Yellow-eyed penguin: erosion of otoliths ans squid beaks. Journal of Field Ornithology 60:451–458.

Hicks DM., Gomez B., Trustrum NA. 2000. Erosion thresholds and suspended sediment yields, Waipaoa River Basin, New Zealand. Water Resources Research 36:1129–1142. DOI: 10.1029/1999WR900340.

Hilton GM., Thompson DR., Sagar PM., Cuthbert RJ., Cherel Y., Bury SJ. 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin Eudyptes chrysocome. Global Change Biology 12:611–625. DOI: 10.1111/j.1365-2486.2006.01130.x

Hinz H., Prieto V., Kaiser MJ. 2009. Trawl disturbance on benthic communities: Chronic effects and experimental predictions. Ecological Applications 19:761–773. DOI: 10.1890/08-0351.1.

Jarman SN., McInnes JC., Faux C., Polanowski AM., Marthick J., Deagle BE., Southwell C., Emmerson L. 2013. Adélie Penguin Population Diet Monitoring by Analysis of Food DNA in Scats. PLoS ONE 8:e82227. DOI: 10.1371/journal.pone.0082227.

Jiang W., Carbines G. 2002. Diet of blue cod, *Parapercis colias*, living on undisturbed biogenic reefs and on seabed modified by oyster dredging in Foveaux Strait, New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 12:257–272. DOI: 10.1002/aqc.495.

Kaiser MJ., Spencer BE. 1994. Fish scavenging behaviour in recently trawled areas. Marine Ecology Progress Series 112:41–50. DOI: 10.3354/meps112041.

King SD. 2008. Breeding success of Yellow-eyed penguins on Stewart Island and off-shore islands 2003-2008. Unpublished report. Yellow-eyed penguin trust, Dunedin, New Zealand.

King SD., Harper GA., Wright JB., McInnes JC., van der Lubbe JE., Dobbins ML., Murray SJ. 2012. Site-specific reproductive failure and decline of a population of the Endangered yellow-eyed penguin: a case for foraging habitat quality. Marine Ecology Progress Series 467:233.

Larned S., Snelder T., Unwin M., McBride G. 2016. Water quality in New Zealand rivers: current state and trends. New Zealand Journal of Marine and Freshwater Research 50:389–417. DOI: 10.1080/00288330.2016.1150309.

Lishman GS. 1985. The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of Zoology 205:245–263. DOI: 10.1111/j.1469-7998.1985.tb03532.x.

Lokkeborg S. 2005. Impacts of trawling and scallop dredging on benthic habitats and communities. FAO Fisheries Technical Papers, 472: 1-58

Markowitz TM., Harlin AD., Würsig B., McFadden CJ. 2004. Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems 14:133–149. DOI: 10.1002/aqc.602.

Mattern T., Ellenberg U., Houston DM., Davis LSLS. 2007. Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins. Marine Ecology Progress Series 343:295–306. DOI: 10.3354/meps06954.

Mattern T., Houston DM., Lalas C., Setiawan AN., Davis LS. 2009. Diet composition, continuity in prey availability and marine habitat – keystones to population stability in the Snares Penguin (*Eudyptes robustus*). Emu 109:204–213. DOI: 10.1071/MU0800.

Mattern T., Ellenberg U., Houston DM., Lamare M., Davis LS., Van Heezik Y., Seddon PJ. 2013. Straight line foraging in yellow-eyed penguins: new insights into cascading fisheries effects and orientation capabilities of marine predators. PloS ONE 8:e84381. DOI: 10.1371/journal.pone.0084381.

Mattern T. 2016. Examining foraging behaviour, prey encounter rates and state of the marine environment using animal-borne camera loggers on Yellow-eyed penguins (45799-FAU). Field report - Pilot Study: December 2015. Dunedin, New Zealand. DOI: 10.13140/RG.2.2.15167.71846.

Mattern T., McPherson MD., Ellenberg U., van Heezik Y., Seddon PJ. 2017a. High definition video loggers provide new insights into behaviour, physiology, and the oceanic habitat of marine top predators. PeerJ Preprints 5:e2765v1. DOI: 10.7287/peerj.preprints.2765v1.

Mattern T., Meyer S., Ellenberg U., Houston DM., Darby JT., Young MJ., van Heezik Y., Seddon PJ. 2017b. Quantifying climate change impacts emphasises the importance of managing regional threats in the endangered Yellow-eyed penguin. PeerJ 5:e3272. DOI: 10.7717/peerj.3272.

Mattern T., Ellenberg U., Davis LS. 2007. Decline for a Delicacy: Are decreasing numbers of Yellow-eyed penguins on Stewart Island a result of commercial oyster dredging. In: 6th International Penguin Conference. Hobart, Tasmania,. DOI: 10.13140/RG.2.2.32178.50884.

Mattlin RH., Scheibling RE., Förch EC. 1985. Distribution, abundance and size structure of arrow squid (*Nototodarus sp.*) off New Zealand. NAFO Scientific Council Studies 9:39–45.

McLeod IM., Parsons DM., Morrison MA., Van Dijken SG., Taylor R. 2014. Mussel reefs on soft sediments: A severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. New Zealand Journal of Marine and Freshwater Research 48:48–59. DOI: 10.1080/00288330.2013.834831.

Meynier L., Morel PCH., Mackenzie DDS., Macgibbon A., Chilvers BL., Duignan PJ. 2008. Proximate composition, energy content, and fatty acid composition of marine species from Campbell Plateau, New Zealand. New Zealand Journal of Marine and Freshwater Research 42:425–437. DOI: 10.1080/00288330809509971.

Ministry of Primary Industries. 2016. Blue Cod (BCO). In: Fisheries Assessment Plenary May 2016: Stock Assessments and Stock Status. Wellington, New Zealand: Ministry of Primary Industries, 127–169.

Ministry of Primary Industries. 2017. Red Cod (RCO). In: Fisheries Assessment Plenary May 2017: Stock Assessments and Stock Status. Wellington, New Zealand: Ministry of Primary Industries, 1061–1072.

Moore PJ., Wakelin MD., Douglas ME., McKinlay B., Nelson D., Murphy B. 1995. Yellow-eyed penguin foraging study, south-eastern New Zealand, 1991-1993. Wellington, N.Z.: Department of Conservation. Available at *http://www.doc.govt.nz/Documents/science-and-technical/sr83a.pdf*.

Moore PJ. 1999. Foraging range of the Yellow-eyed penguin *Megadyptes antipodes*. Marine Ornithology 27:49–58.

Moore PJ., Wakelin MD. 1997. Diet of the Yellow-eyed penguin *Megadyptes antipodes*, South Island, New Zealand, 1991-1993. Marine Ornithology 25:17–29.

Mullan AB., Wratt DS., Renwick JA. 2002. Transient Model Scenarios of Climate Changes for New Zealand. Weather and Climate 21:3–34.

Murphy RJ., Pinkerton MH., Richardson KM., Bradford-Grieve JM., Boyd PW., Bradford-Grieve JM., Boyd PW. 2001. Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. New Zealand Journal of Marine and Freshwater Research 35:343–362. DOI: 10.1080/00288330.2001.9517005.

Norman MD., Reid AL. 2000. A guide to squid, cuttlefish and octopuses of Australasia. Collingwood, VIC: CSIRO Publishing.

NZ Ministry of Fisheries. 2007. Red Cod (RCO 3) – Final Advice. In: Fisheries Management System Review 2007. Wellington, New Zealand: NZ Ministry of Fisheries, 270–291.

Paulin C., Stewart A., Roberts C., McMillan P. 2001. New Zealand Fish - A CompleteGuide. Wellington, New Zealand: Te Papa Press.

Queirós AM., Hiddink JG., Kaiser MJ., Hinz H. 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. Journal of Experimental Marine Biology and Ecology 335:91–103. DOI: 10.1016/j.jembe.2006.03.001.

Richardson AJ., Bakun A., Hays GC., Gibbons MJ. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology & Evolution 24:312–322. DOI: 10.1016/j.tree.2009.01.010.

Schratzberger M., Jennings S. 2002. Impacts of chronic trawling disturbance on meiofaunal communities. Marine Biology 141:991–1000. DOI: 10.1007/s00227-002-0895-5.

Seddon PJ., van Heezik Y. 1990. Diving Depths of the Yellow-eyed penguin *Megadyptes antipodes*. Emu 90:53–57.

Smith PJ., Mattlin RH., Roeleveld MA., Okutani T. 1987. Arrow squids of the genus nototodarus in new zealand waters: Systematics, biology, and fisheries. New Zealand Journal of Marine and Freshwater Research 21:315–326. DOI: 10.1080/00288330.1987.9516227.

Talley's Group Limited. 2018. Blue cod. https://www.talleys.co.nz/about-us/divisions/seafood/products/fish/#blue-cod. Accessed 12. 05. 2018

Thompson DR., Bury SJ., Hobson KA., Wassenaar LI., Shannon JP. 2005. Stable Isotopes in ecological studies. Oecologia 144:517–519.

Thrush SF., Dayton PK. 2002. Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annual Review of Ecology and Systematics 33:449–473. DOI: 10.1146/annurev.ecolsys.33.010802.150515.

Trathan PN., García-Borboroglu P., Boersma D., Bost C-A., Crawford RJM., Crossin GT., Cuthbert RJ., Dann P., Davis LS, De La Puente S., Ellenberg U., Lynch HJ., Mattern T., Pütz K., Seddon PJ., Trivelpiece W., Wienecke B. 2015. Pollution, habitat loss, fishing, and climate change as critical threats to penguins. Conservation Biology 29:31–41. DOI: 10.1111/cobi.12349.

Turner SJ., Thrush SF., Hewitt JE., Cummings VJ., Funnell G. 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management and Ecology 6:401–420. DOI: 10.1046/j.1365-2400.1999.00167.x.

Walling DE. 2006. Human impact on land–ocean sediment transfer by the world's rivers. Geomorphology 79:192–216. DOI: 10.1016/j.geomorph.2006.06.019.

Wilson RP. 1984. An improved stomach pump for penguins and other seabirds. Journal of Field Ornithology 55:109–111.

Wilson RP., La Cock GD., Wilson M-P., Mollagee F. 1985. Differential Digestion of Fish and Squid in Jackass Penguins S*pheniscus demersus*. Ornis Scandinavica 16:77. DOI: 10.2307/3676580.

Yang YW., Frazer A., Rees E. 2010. Self-governance within a QMS framework—The evolution of self-governance in the New Zealand Bluff oyster fishery. Marine Policy 34:261–267. DOI: 10.1016/j.marpol.2009.07.003.