The jellyfish buffet: jellyfish enhance seabird foraging opportunities by concentrating prey

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High levels of jellyfish biomass have been reported in marine ecosystems around the world, but understanding of their ecological role remains in its infancy. Jellyfish are generally thought to have indirect negative impacts on higher trophic-level predators, through changes in lower trophic pathways. However, high densities of jellyfish in the water column may affect the foraging behaviour of marine predators more directly, and the effects may not always be negative. Here, we present novel observations of a diving seabird, the thick-billed murre, feeding on fish aggregating among the long tentacles of large jellyfish, by using small video loggers attached to the birds. We show that the birds encountered large jellyfish, Chrysaora melanaster, during most of their dives, commonly fed on fish associated with jellyfish, and appeared to specifically target jellyfish with a high number of fish aggregating in their tentacles, suggesting the use of jellyfish may provide significant energetic benefits to foraging murres. We conclude that jellyfish provide feeding opportunities for diving seabirds by concentrating forage fish, and that the impacts of jellyfish on marine ecosystems are more complex than previously anticipated and may be beneficial to seabirds.

1. Introduction

High levels of jellyfish biomass have been reported in marine ecosystems around the world [1], which is often referred to as a ‘jellyfish bloom’ [2]. Jellyfish blooms are expected to have large impacts on marine ecosystems. For instance, jellyfish consume substantial amounts of lower trophic-level prey (e.g. up to 50.1% of the zooplankton standing stock in the Bering Sea [3]), and may indirectly affect higher trophic-level predators through changes in trophic pathways [4]. On the other hand, jellyfish may directly affect the immediate foraging environment of marine predators, not only for those feeding on jellyfish [5,6], but also for those feeding on jellyfish-associated prey. For example, high densities of jellyfish in the water column [3] may affect the foraging behaviour of piscivorous predators by changing the fine-scale distribution of fish schools [6,7]. However, few studies have examined the direct impact of jellyfish on the foraging behaviour of marine predators owing to technological limitations in observing underwater foraging behaviour.

Large-scale jellyfish blooms have been documented in the Bering Sea since the early 1990s [3], a region renowned for its high concentrations of foraging seabirds [8]. During a jellyfish bloom in 1995, densities of jellyfish reached $11.3 \pm 3.2$ individuals $m^{-3}$ [9]. Previous studies have reported interactions between jellyfish and fish, where juvenile fish swim among the tentacles of large jellyfish to feed on zooplankton captured by jellyfish and/or jellyfish...
tissues, or to use the biotic structure of jellyfish to avoid predators [9,10]. This aggregation of fish, and thus jellyfish, may provide high-density prey patches for piscivorous seabirds [1,4]. Recently, animal-borne video loggers have become a powerful tool to observe the at-sea behaviour of free-ranging marine predators [11,12]. In this study, we present novel observations of foraging interactions among seabirds, fish and jellyfish in the Bering Sea, by using newly developed bird-borne video loggers.

2. Material and methods

We studied a free-ranging diving seabird, the thick-billed murre (Uria lomvia), on St George Island (56°35′ N, 169°35′ W), in the eastern Bering Sea, Alaska, USA, in August 2014. We used a video logger (DVL-200, Little Leonardo, Japan) to obtain video footage of underwater foraging behaviour, and also used time–depth–temperature–acceleration data loggers (ORI400-D3GT, Little Leonardo, Japan or Axy-Depth, TechnoSmaRt, Italy) to obtain behavioural and environmental data.

We attached loggers to eight chick-rearing birds. Video loggers recorded for 2.5 h, but the video footage from four of the eight birds did not record any underwater behaviour. We visually inspected the video footage (in total 10 h of observations from four birds), which covered 97 daytime dives (09:00–13:00 local time). From two of four birds, we also obtained behavioural and environmental data (data from the other two birds were not available owing to a technical problem with the loggers). Specifically, we extracted the wing stroking behaviour, and calculated the changes in vertical speed during each dive from depth–acceleration data (see detail in electronic supplementary material). We estimated the vertical profile of water temperature, to examine the thermocline depth [13]. These behavioural and environmental data were analysed using IGOR PRO software (Wave Metrics, USA). We examined the effect of the number of fish among the tentacles of jellyfish on the probability of attack by the birds, by using generalized linear-mixed models (GLMMs) with binomial distribution, including bird ID as a random factor. Akaike’s information criterion corrected for small sample size was used to compare the models (AICc), which does not support

3. Results

The birds dove to 78.2 ± 5.9 m (n = 38 dives) and for 150 ± 23 s (n = 97 dives) on average; performing U-shaped dives with clear descent, bottom and ascent phases, typical for this species [14]. The video footage was too dark to observe during the bottom phase of the dives, but was light enough for visual inspection from sea surface down to a depth of 35 m (0–34.5 ± 3.1 m) during the descent phase, and from 66 m to the sea surface (66.1 ± 4.7–0 m) during the ascent phase.

In the video footage, we observed 197 feeding events (on fish: 174; krill: 8; unknown prey: 15) during the ascent phase, but none during the descent phase. The birds took, on average, 2.4 ± 1.6 prey items per ascent phase (among the four individuals, mean values ranged from 1.7 to 3.2 prey per ascent). We also observed 179 encounters between the birds and large jellyfish during the ascent phase of 82 dives, which represented 85% of all recorded dives (ranging from 78% to 100% of dives per individual; electronic supplementary material, movie S1). We identified the jellyfish as Chrysaora melanaster (based on body size and number of tentacles [15]), a typical species occurring in the Bering Sea [3,9]. Forty-nine out of 179 jellyfish had juvenile fish (mainly age-0 walleye pollock, TL < 50 mm; based on the comparison of fish size to the bird’s beak size) among their tentacles, with the number of fish among the tentacles varying widely (6.9 ± 6.7 fish). In 19.7% of all fish-feeding events (ranging from 7.9% to 23.4% per individual), we observed that all four focal individuals approached jellyfish and fed on fish swimming around their tentacles (electronic supplementary material, movie S2). In the other fish-feeding cases, birds fed on solitary fish not associated with jellyfish (electronic supplementary material, movie S3). Encounter events with jellyfish and fish occurred at depths below the thermocline (figure 1a).

During the descent and bottom phases, birds stroked their wing actively to swim, whereas birds did not stroke but passively floated to the sea surface during the ascent phase, a pattern typical for this species (figure 2) [16]. However, birds did stroke frequently and decreased vertical speed when they fed on prey during the ascent phase (figure 2). Birds did not always feed on juvenile fish associated with jellyfish and occasionally by-passed jellyfish with fish without any feeding events. We examined the effect of number of jellyfish-associated fish on feeding behaviour of birds and found that the probability of attack towards fish (defined by the bird’s head moving towards prey) increased as the number of fish among the tentacles increased (figure 2 and table 1). Additionally, birds did not feed on more than one fish from a patch associated with the same jellyfish. In 38.2% of all feeding events associated with jellyfish (13 of 34 events), juvenile fish appeared to disperse (we defined ‘disperse’ as ‘fish swim away from tentacles of jellyfish’) in response to a bird’s attack.

4. Discussion

Our bird-borne video observations showed that the jellyfish C. melanaster are prevalent in the eastern Bering Sea where thick-billed murres forage. This corresponds to a ship-based survey showing relatively high jellyfish biomass in the eastern Bering Sea in 2014 [17].

The birds showed a novel behaviour, feeding on juvenile fish associated with jellyfish, in approximately 8–23% of all fish-feeding events. Although our sample sizes were small, such feeding behaviour appears to be common at least for birds breeding on St George Island, as all four focal birds showed this behaviour. This feeding behaviour occurred at depths well below the thermocline (figure 1a), which does not support previous studies suggesting that foraging at the thermocline depth is typical for thick-billed murres in the Bering Sea [13]. Birds might use the depth zones below the thermocline for hunting fish associated with C. melanaster. Additionally, we never observed schooling fish except those associated with jellyfish. We suggest that, as jellyfish numbers increase, they provide ample foraging opportunities for diving seabirds by concentrating prey in dense, easily exploitable patches at depths independent of the thermocline (figure 1a).

Diving seabirds are generally considered to feed only during the bottom phases of dives, not while in transit to the bottom during the descent and ascent dive phases [18]. However, thick-billed murres in our study clearly captured prey during the ascent phase (electronic supplementary material, movie S1).
The birds changed their wing stroking patterns during the ascent phase, indicating active feeding by changing body angles and lingering at certain feeding depths (figure 2). They might be able to use positive buoyancy to approach and capture fish more easily during the ascent phase [19]. Our estimates (see details in the electronic supplementary material), based on prey energy content and measurements of daily energy expenditures of thick-billed murres breeding on St George Island [8], suggest that the energy obtained during ascent may account for 25.8–45.4% of the daily energy needs of a chick-rearing thick-billed murre.

Previous studies suggested that juvenile fishes aggregate among the tentacles of jellyfish to avoid predators [9]. Our observations showed that dense patches of fish associated with jellyfish attract foraging murres (figure 1b). Furthermore, in response to a bird’s attack fish dispersed away from, rather than hid in, the jellyfish’s tentacles. Although it is possible that individual fish are less prone to predation owing to the dilution of predation risk when a large number of fish aggregate in a school, it is more likely that fish are attracted to feed on zooplankton captured by jellyfish [9] and/or passively aggregate among the tentacles of jellyfish.

In conclusion, thick-billed murres obtain a significant amount of fish that are aggregated around jellyfish in the Bering Sea. We suggest that, in addition to altering trophic web dynamics, recent jellyfish blooms may create new feeding opportunities for some top predators through the foraging

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**Table 1.** Model selection results and parameter estimates for GLMM (with binomial distribution) fitted to the probability of bird’s attack towards fish ($n = 139$ events). Bird ID ($n = 4$ birds) was included as a random factor in the models.

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<td>1.0</td>
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<td>4.20</td>
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<td>intercept</td>
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<td>0.42</td>
<td>-5.65</td>
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**Figure 1.** (a) Vertical changes in the water temperature (i). Vertical distribution of encounter events with solitary juvenile fish (ii), jellyfish without fish (iii) and jellyfish with fish (iv) for 36 dives from two birds where both video and diving behaviour data were collected. The estimated depth of the thermocline was from 9.6 to 24.8 m. (b) Effect of number of fish among tentacles of jellyfish (x-axis) on the probability of attack behaviour of birds towards fish (y-axis). Occurrence/non-occurrence of attack behaviour was determined by the bird’s head movements towards prey. The probability of attack increased as the number of fish among the tentacles of a jellyfish increased. Please see table 1 for the statistical results. (Online version in colour.)
interactions among seabirds, fish and jellyfish. These observations suggest that the impacts of jellyfish blooms on marine ecosystems are more complex than previously anticipated and might be beneficial at least to some seabirds.

Ethics. This work has been performed under all required USA Federal, State and special use permits. Bird capture and methods of logger attachment have been approved by the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks.

Data accessibility. Raw data were uploaded as the electronic supplementary material.

Authors’ contributions. N.S., Y.W., A.S.K., A.T. conceived and designed the research. N.S., N.K., T.Y. performed the field study. N.S. analysed the data. N.S., A.S.K. and A.T. wrote the paper. All authors provided input and approved the paper.

Competing interests. We declare we have no competing interests.

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Figure 2. Changes in depth, heaving acceleration, vertical speed and wingbeat frequency during typical dives of thick-billed murres. The bird stroked its wings continuously during the descent and bottom phases (a,b). However, during the ascent phase, birds scarcely stroked and ascended with a constant vertical speed when there were no feeding events (c). In contrast, when birds fed on prey during ascent (d, arrowhead), the number of wing strokes increased up to 2 Hz, and vertical speed decreased instantaneously (d). (Online version in colour.)


