

Investigating the functional link between prey abundance and seabird predatory performance

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ABSTRACT: Investigating the relationships that link marine top predators and their prey is crucial for an understanding of the mechanisms that operate within marine food chains. Many seabird species capture their prey underwater, where direct and continuous observation is difficult. However, in a captive setting, predator–prey interactions can be studied under controlled conditions and in great detail. Using an underwater video-array, we investigated the prey–capture behaviour of a foot-propelled pursuit diver, the double-crested cormorant *Phalacrocorax auritus*, targeting juvenile rainbow trout *Oncorhynchus mykiss*. We tested the effects of prey density, prey size, light conditions and prey behaviour (schooling vs. solitary trout) on the foraging performance of 9 cormorants. As predicted, prey density exerted the strongest influence on cormorant foraging success. While we found an apparently linear relationship between prey density and prey capture rate, a density below the threshold of about 2 g m⁻³ resulted in disproportionately lower catch per unit effort (CPUE) values. If such a threshold density exists in a natural setting, it could have important implications for birds confronted with a decline in food abundance, when density levels will be reduced. We also demonstrate the marked impact of fish behaviour on the predatory performance of cormorants. Capture success of cormorants was significantly lower and pursuit duration significantly higher when birds attacked schooling rather than solitary trout. By contrast, prey size and light conditions did not have a measurable effect on cormorant prey–capture performance. Our study is an experimental investigation into the prey–capture performance of an avian pursuit diver within a captive setting. We provide input values that should be incorporated into ecological models, which might help to understand predator requirements in a changing environment.

KEY WORDS: Prey–capture performance · Prey density · Functional relationship · Predator–prey interaction · Marine food chain · Foraging · Double-crested cormorant

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INTRODUCTION

Predatory fish, seabirds and marine mammals are key players at the top of marine food chains and structure marine ecosystems across a wide range of spatial and temporal scales. To understand these complex systems, it is important to study the relationships between predators and prey. How does prey abundance and behaviour affect predatory performance? Knowledge of the functional link between these variables is crucial if we want to model marine ecosystems

and their response to environmental change. However, direct observation of marine top predators foraging underwater is a challenging task, hampered by numerous practical difficulties and is therefore rare (see for example: Similä & Ugarte 1993, Axelsen et al. 2001). In the last two decades many of these difficulties have been overcome through the development of miniaturized electronic devices (data loggers), which can be attached to animals foraging in the wild (for review see Ropert-Coudert & Wilson 2005). While this has permitted the collection of information regarding the overall

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foraging patterns of marine predators (location, dive depth, dive duration etc.), little is known about predator–prey interactions on a fine scale. In fact, although we have learnt a considerable amount about the behaviour of predators, we know little about their behaviour in relation to that of their prey. Recently, animal-mounted underwater cameras have been deployed (Davis et al. 1999, Bowen et al. 2002, Takahashi et al. 2004, Grémillet et al. 2006) and allow us a glimpse into the underwater behaviour of these animals. Currently, however, most of these cameras are either relatively large, restricting deployment to larger-sized species, or allow only infrequent sampling. While other techniques are currently being developed (e.g. Axelsen et al. 2001), continuous direct observation of marine top predators foraging in the wild is still difficult. Until logistic difficulties can be overcome, captive studies can serve as a proxy for the natural situation. In a captive setting a variety of factors that might shape the fine scale foraging behaviour of a predator but which are difficult to control in the field, can be altered systematically, which allows the study of predator–prey interactions in great detail. Some of the factors that might constrain the fine scale foraging behaviour of a diving predator and were investigated in the current study are:

(1) Prey density: Probably the most critical factor determining predator foraging success. Holling (1959) predicted a functional link between the foraging success of vertebrate predators and prey density (defined as the functional response). For aquatic birds foraging on fish it has been shown that foraging success increases with prey density in form of a hyperbolic shaped curve, similar to the type II curve of Holling's model (Wood & Hand 1985, Draulans 1987, Ulenaers et al. 1992). This suggests that at high prey densities, the intake rate of a predator might be limited by its ability to handle and digest prey. In contrast, if prey density is low, a predator might have to spend an increased amount of time and energy to locate and capture prey in sufficient amounts. A threshold density might exist, below which sustainable foraging (i.e. the predator is able to meet its energetic requirements) might become impossible.

(2) Prey size: While there are obvious limitations on the size of prey that a predator can swallow, size also has implications for the locomotor performance of a prey species and its ability to escape a predator. Larger fish of a given species can reach higher steady speeds than smaller individuals (Beamish 1978). It might therefore be easier for a predator to catch a smaller fish of a given species, rather than a larger fish after a prolonged chase. In contrast, the speed achieved within a given time, an important parameter during predator–prey encounters, is size independent, while manoeuvr-

ability decreases with body length (for review see Domenici & Blake 1997, Domenici 2001). Also, from the predator's perspective, Domenici (2001) suggested that acceleration performance in vertebrates declines with size, when a larger size range is considered. Hence, overall manoeuvrability and acceleration of small prey might be superior to that of a large predator and make it easier for small prey to escape.

(3) Light levels: Most avian divers are visual predators and rely on sight to locate and capture their prey. During diving they experience a decrease in illumination with increasing depth because of scatter and absorption of light by water molecules and suspended particles (turbidity). Consequently, image brightness and contrast degrade rapidly with increasing depth and/or turbidity (Strod et al. 2004). The amount of light available during foraging is therefore likely to be an important factor that might restrict foraging to periods with sufficient light or areas with low turbidity.

(4) Prey behaviour: A number of behavioural patterns evolved in prey species that decrease the likelihood of being captured by a predator. Schooling is one such important anti-predator behaviour in many fish species. It provides protection from predators through a number of mechanisms (see Pitcher & Parrish 1993 for review but also Axelsen et al. 2001 for an alternative view). Targeting schooling prey might have important consequences for a predator since it might be more difficult to pursue and capture an individual within a school, and hence, decrease the foraging success (e.g. prey–capture rate) of a predator.

For practical reasons, experimental investigation of predator–prey interactions in the aquatic environment has been principally restricted to fish (Neil & Cullen 1974, Turesson & Broenmark 2004), while studies on diving birds or mammals are rare. In the few studies that experimentally investigated the foraging behaviour of aquatic birds (Wood & Hand 1985, Ulenaers et al. 1992, Fox 1994), observation was restricted to surface behaviour, omitting all underwater activity from analysis (i.e. search, pursuit, capture, handling). To investigate the importance of the factors introduced above on predator performance, we studied the prey–capture behaviour of double-crested cormorants *Phalacrocorax auritus albociliatus* foraging on juvenile rainbow trout *Oncorhynchus mykiss* using an underwater video array. Double-crested cormorants are foot-propelled pursuit divers that forage on both benthic and pelagic fish. Along the Pacific coast of North America they utilise a variety of marine and freshwater habitats, where they target their prey in the upper part of the water column (typically <20 m). Diet composition strongly reflects habitat use and pelagic/schooling fish species (especially salmonids) make up a substantial part of the prey biomass ingested in estuarine

areas (Collis et al. 2002, Anderson et al. 2004). In the Pacific Northwest, cormorants also prey on juvenile salmonids, such as rainbow trout, which are released from hatcheries as part of salmonid enhancement programs. Given their enormous population growth since the 1970's, double crested cormorants have acquired a negative public image and, in some parts of North America, are currently perceived as a pest species that very effectively catches huge amounts of fish. However, little is known about the factors that condition their foraging success.

Hence, the purpose of our study was to investigate factors affecting cormorant foraging performance. We studied the underwater foraging behaviour of double-crested cormorants targeting rainbow trout of different size and at different prey densities. The effects of fish behaviour (schooling vs. solitary) and light conditions on cormorant prey-capture performance were also investigated.

MATERIALS AND METHODS

Nine adult or sub-adult double-crested cormorants (minimum age 2 yr) with a mean body mass of 2.10 ± 0.16 kg (mean \pm SD, range 1.81–2.47 kg) were used in this study. Eight of the birds had been captured as chicks (5 to 6 wk of age) from the breeding colony on Mandarte Island (southwestern British Columbia, Canada). One bird had been bred in our captive setting. All birds were well established in captivity and were housed communally in sheltered outdoor pens (8 m long \times 4 m wide \times 5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC) in Vancouver. Birds were fed approximately 10% of their body mass daily with a mixed diet consisting of Pacific herring *Clupea pallasii* and rainbow smelt *Osmerus mordax*, supplemented with vitamin B1 tablets (thiamine hydrochloride, Stanley Pharmaceuticals). Body mass was determined regularly to the nearest 10 g when birds were post-absorptive and dry, using a digital spring balance (UWE, HS-15K; Universal Weight Enterprise). All birds maintained a stable body mass throughout our study (Jun to Nov 2003). All experimental procedures were approved by the UBC Animal Care Committee (Animal Care Certificate # A02-0122) and were in compliance with the principles promulgated by the Canadian Council on Animal Care.

Video set-up. An underwater video array was set up within a cylindrical deep dive tank (5 m in diameter, 10 m water depth), consisting of 8 black and white video cameras (Model CVC6990, a light sensitive, submersible camera with a 3.6 mm wide angle lens; minimum illumination 0.01 lux; Lorex, MBrands), 2 multi-

plexers (EverFocus Electronics), a video date time generator (RCA, Thompson Multimedia), 2 video recorders (Sony) and 2 video monitors (Citizen). The cameras were mounted at various positions within the dive tank (Fig. 1), with overlapping visual fields providing complete visual coverage. The video signals of the cameras were fed into 2 multiplexers, which projected the images onto 2 video monitors (4 cameras per monitor). One multiplexer was equipped with an internal clock (resolution: 1 s) while the signal of the other multiplexer was fed into a video date time generator (resolution: 0.1 s). Both clocks were synchronized before a series of trials started and were recorded together with the images on VHS tape. During the trials birds were observed from within a small observation hut on top of the dive tank, which housed all video equipment (Fig. 1).

Fish. Juvenile rainbow trout (total length [TL]: 15 to 22 cm, body mass [M_b]: 23 to 92 g) were obtained from

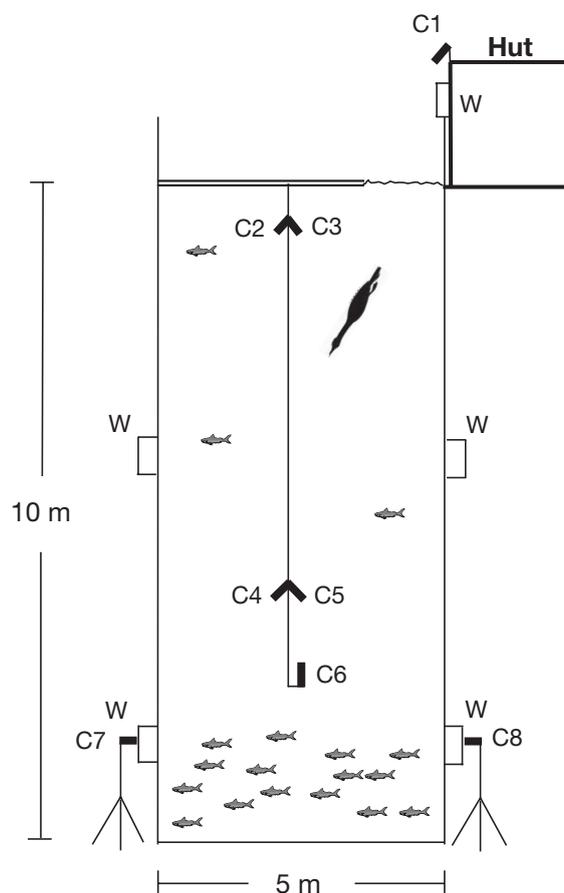


Fig. 1. Video camera setup in the deep dive tank indicating the position of the 8 black and white video cameras (C1–C8). Tank dimensions (with a total water volume of 196 m^3), windows (W), a diving cormorant and a typical fish distribution at the beginning of a series of trials (when fish density was highest) are also indicated

the Fraser Valley Trout Hatchery (British Columbia) in June 2002 and kept in de-chlorinated, fully aerated Vancouver city tap-water. Upon arrival fish were caught, weighed (to the nearest g), measured (to the nearest 0.5 cm) and sorted into 2 size classes ('small fish' with $M_b \geq 50$ g and $TL \geq 18.5$ cm, and 'large fish' with $M_b < 50$ g and $TL < 18.5$ cm) which were kept in separate holding tanks. Water temperature in the tanks varied according to season and ranged between 6°C in winter and 15°C in summer. Fish were fed commercial trout food daily (Jamieson's Feed) until used in experiments.

At least 3 d before conducting trials, the dive tank was filled with chlorinated Vancouver city tap-water. To eliminate the chlorine, air was bubbled through the tank for at least 2 d before any fish were introduced into the tank. Chlorine levels were checked before fish introduction and were always less than 0.05 mg l⁻¹, well below a level that might affect fish. Water inside the dive tank was standing, so that temperature fluctuated more widely than within the fish holding tanks, where a continuous flow was maintained. However, the temperature difference between the fish holding tanks and the dive tank rarely exceeded 5°C. Every morning, before a set of trials, 15 to 23 'small' or 'large' trout were caught, weighed and measured (to ensure proper classification and to calculate the mean fish size inside the dive tank) and introduced to the bottom of the dive tank by means of a PVC tube and a plunger. To allow fish to accommodate to the new environment, they were introduced at least 2 hr before the start of the trials. A variety of structures (concrete blocks, PVC tubes and other items) were placed at the bottom of the tank to provide hiding places for the fish. While fish made use of these structures, they generally roamed throughout the tank. Fish often started to school when the overall number of fish within the dive tank was large (>10 ind.). We defined a school as a group of fish that swam together, while often displaying a variable degree of polarization, synchronization and density (Pitcher & Parrish 1993, Viscido et al. 2004).

Training protocol and trials. Birds were trained to dive for live juvenile rainbow trout of varying size and density within our setup for at least 3 wk before data collection began. Each bird was caught in its holding pen and introduced into the dive tank, where it started to dive immediately. All underwater and surface activity during the trial was filmed. After capture of a number of fish a bird usually left the water and wingspread for some time, often starting another foraging bout towards the end of the 30 min trial. At the end of a trial the bird was caught and returned to its holding pen. Each bird participated in 1 trial d⁻¹, with a maximum of 5 birds participating in the daily trials, which were conducted in series.

One important factor to consider when conducting foraging behaviour experiments with captive animals is motivation. If the motivation of an animal to forage and capture prey fluctuates too much between trials, it will likely result in a variable foraging performance. In an attempt to keep bird motivation during the trials similar over the course of data collection, we kept the daily amount of food ingested by a bird constant. The amount needed for each bird to maintain motivation was established during the training trials. When the daily trials were completed, birds were handfed their remaining daily allotment. Birds were then deprived of food for at least 17 hr before a new set of trials started. Consequently, all birds cooperated well during the period of data collection and seemed highly motivated to capture live fish.

In addition to filming, the following variables were recorded: (1) air temperature was measured at the start of each trial, while (2) water temperature was measured at the end of a set of trials just below the water surface and at the bottom of the tank. (3) Underwater illumination was obtained from a light attenuation profile (at 1, 5, and 10 m water depth) taken at the end of every foraging trial using the GeoLT data logger (Earth&Ocean Technologies), which recorded illuminance (resolution at 100 lx was 0.03 lx). (4) Fish density (g m⁻³ or number of fish m⁻³) was calculated as the overall fish mass (or number of fish) inside the dive tank at the start of a trial divided by water volume (196 m³). (5) Mean size of fish for each trial day was calculated as the mean size of the trout introduced into the dive tank in the morning. Occasionally birds did not eat all the fish that had been introduced into the dive tank in the morning. The exact number of fish left over was counted via the video set-up the following morning and checked against our records. Fish density in the dive tank was then balanced by introducing relatively fewer fish of the same size class for that day. Size of the individuals left over was taken as the mean size from the day before.

Video analysis. Videotapes were viewed and all dive and surface times within a 30 min trial were marked down to the nearest second. Each dive cycle (dive and subsequent surface interval) was split into the following behavioural categories: searching, prey pursuit, prey handling, resting at the surface. For each behavioural category observed, start and end time as well as duration was noted to the nearest second. By definition a bird was 'searching' during a dive until it started a 'prey pursuit' or surfaced. Prey pursuit was identified as a response by the bird to the fish, typically signaled by a change in swim direction or speed (as indicated by an increase in foot stroke frequency). Prey pursuit ended either when the bird caught a fish or when it 'gave up', as indicated by a change in swim direction or speed (slowing of

stroke frequency). After an unsuccessful prey pursuit the bird, by definition, continued 'searching' until it either initiated a new prey pursuit or surfaced. 'Prey handling' was defined as the time between prey capture and prey ingestion. 'Rest at surface' marked the time spent at the surface between consecutive dives. Additionally, we recorded fish distribution within the dive tank, whether or not fish were schooling, the response of a single fish or school to an approaching bird, whether birds pursued individuals or a school, the number of fish caught and depth of their capture.

Factors affecting prey-capture performance. We investigated the effect of the following factors on cormorant prey-capture performance:

(1) Prey density: Prey density was assessed as the overall fish density within the tank. Fish density at the beginning of a series of daily trials was kept constant ($\sim 7 \text{ g m}^{-3}$ or $\sim 0.12 \text{ fish m}^{-3}$). The fish density that a bird encountered during a trial was altered by randomly changing the bird's position within the daily trial order. Fish density was highest at the beginning of the first trial of the day and declined as birds caught and ingested fish, so that fish density was lowest during the last trial of the day. The effect of fish density on cormorant foraging success was assessed by computing prey capture rates during a trial (catch per unit effort or CPUE, in g fish caught s^{-1} submerged) vs. fish density (g m^{-3}) at the beginning of that trial. We also assessed the effect of fish density on search time and prey encounter rate. Our density assessment does not reflect the actual packing density within schools that formed frequently, which was far greater. We did not investigate the effects of a change in packing densities within schools on cormorant foraging performance. Hence, in the strict sense, our prey density assessment represents fish abundance.

(2) Prey size: We investigated the effect that fish size might have on predator performance. The size of trout introduced into the dive tank was systematically altered, while trial days with 'small' ($M_b \geq 50 \text{ g}$, $TL \geq 18.5 \text{ cm}$) or 'large' ($M_b < 50 \text{ g}$, $TL < 18.5 \text{ cm}$) fish were chosen at random. Predatory performance was assessed by computing CPUE values for trials of both size classes with similar fish densities and by plotting these CPUE values against mean fish size during the corresponding trials. We also computed the success rate of initiated prey pursuits and the duration of successful pursuits (as an indication of foraging effort) for both fish size classes.

(3) Light conditions: To investigate if the predatory performance of cormorants might be limited by the available light, we altered light conditions encountered by the birds underwater. This was achieved by conducting trials either around midday, when light conditions were best (max. 120 lx at 10 m depth, com-

parable with workspace lighting), or in the late afternoon, when light conditions deteriorated (min. 1.8 lx at 10 m depth, comparable with full moon lighting). Water inside the tank was clear with a turbidity of about 0.5 NTU (nephelometric turbidity units) during all trials.

(4) Fish behaviour (schooling vs. solitary trout): During the training trials we observed that fish often started to school inside the dive tank and this appeared to affect predator behaviour. Hence, in our video analysis we distinguished a 'schooling' from a 'non-schooling' situation. By definition, in a non-schooling situation the bird targeted an individual fish that was not part of a school (although a school might have existed elsewhere within the tank). In contrast, in a schooling situation the bird targeted the school or an individual that was part of the school. Predatory performance was assessed by computing success rate (percentage of successful pursuits and dives) and the duration of successful pursuits (as an indication of foraging effort), contrasting a schooling and non-schooling situation.

Statistical analysis. All statistical analysis was performed using SigmaStat (Jandel Scientific) and Systat (SPSS) software. The effects of fish density, fish size, light conditions, and fish behaviour on cormorant foraging performance (CPUE) were tested using residual maximum likelihood analysis (REML; Patterson & Thompson 1971). In this analysis, the investigated 4 parameters were entered as fixed factors and bird as a random factor. The effects of the investigated parameters on cormorant foraging performance were determined by comparing Wald statistics with F -distributions. When single comparisons were made, as in comparing the success rate for individual pursuits when birds attacked schooling or non-schooling fish, Student's paired t -test was used. All percentage values were normalised by arcsine transformation beforehand. Significance was accepted at $p < 0.05$. Regression lines for Fig. 2 were fitted using a 'broken-stick-model' (software by J. Lignon and J. L. Rodeau, DEPE Strasbourg). The relationship between fish density and prey capture rate (CPUE) that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz & Slinker 1990). Values given are grand means established from individual bird means and are presented with standard deviation (\pm SD).

RESULTS

Between late August and early November 2003 a total of 82 foraging trials were conducted with 9 birds. During these trials, birds performed a total of 624

dives, lasting between 3 and 49 s (i.e. similar to dive durations observed in the wild). A bird typically began diving within 30 s of introduction into the tank. If prey was encountered, the bird usually started a pursuit which ended either with the capture of the trout, a switch to pursuing another trout, or the bird 'gave up' and returned to the surface. A bird typically dived until either assumed to be 'satiated' (after multiple prey ingestions) or 'frustrated' (if no prey was encountered

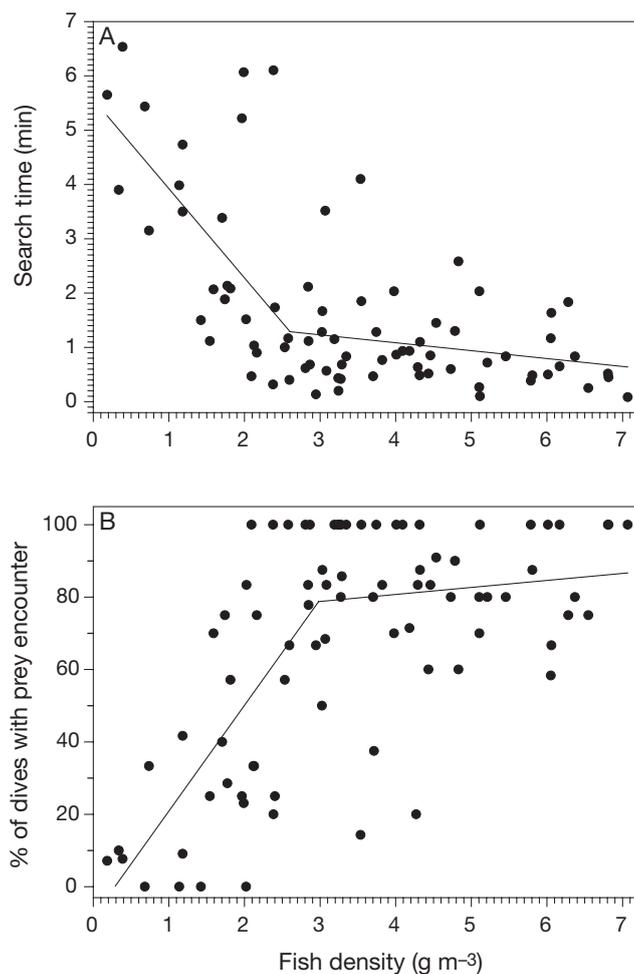


Fig. 2. Underwater search time during a trial and prey encounter rate in relation to fish density. (A) A threshold fish density seems to exist between 2 and 3 g m⁻³, below which the amount of time a cormorant spent searching during a trial increased. The indicated relationship is best described by: $y = -1.64(x - t) - 0.15t + 1.67$ for $x < t$ and $y = -0.15x + 1.67$ for $x > t$, where t is the break point, calculated to be at 2.92 g m⁻³ ($F = 48.84$, $p < 0.0001$, $r^2 = 0.49$, $N = 9$ birds, $n = 77$ trials). (B) The likelihood of a bird encountering a fish during a dive decreased below this threshold fish density. The indicated relationship is best described by: $y = 29.22(x - t) + 1.94t + 72.98$ for $x < t$ and $y = 1.94x + 72.98$ for $x > t$, where t is the break point, calculated to be at 2.98 g m⁻³ ($F = 27.68$, $p < 0.0001$, $r^2 = 0.52$, $N = 9$ birds, $n = 82$ trials)

or caught) and left the water afterwards to wingspread. In the first situation a bird typically started another dive bout towards the end of the 30 min trial. A bird that failed to capture prey performed exploratory dives every now and then, before finally 'giving up' and remaining out of the water, if no prey was encountered or caught in subsequent dives.

We observed 518 prey pursuits of which 275 ended in the capture and ingestion of trout. Mean success rate of all pursuits by the 9 birds was $58.3 \pm 21.0\%$ (range: 31.0 to 92.9%). Since birds often initiated >1 prey pursuit per dive, success rate was higher when expressed on a per dive basis, with a mean of $77.7 \pm 14.5\%$ of all dives during which prey was encountered and pursued being successful. In total, $51.2 \pm 12.3\%$ of all dives conducted ended with the capture and ingestion of a trout. Mean duration of pursuits that ended with prey capture was 6.77 ± 1.48 s (range: 1 to 28 s). Unsuccessful pursuits lasted on average 6.28 ± 1.58 s (range: 1 to 24 s) before birds gave up. While pursuits were initiated throughout the water column, 60% occurred near the bottom of the tank (~8 to 10 m depth), where 53% of all prey was captured. Of prey captures, 21 and 26% occurred near the top (~0 to 2 m depth) and mid-water, respectively. In the final phase of the attack, after closing in on the fish, a bird grabbed the fish at a position posterior to its operculum. The angle of attack during prey capture was about perpendicular to fish orientation and birds displayed a great flexibility in head and neck motion during this phase. Fish often thrashed vigorously after capture, so that birds readjusted their grip, positioning the fish perpendicular to their own body axis inside their beak, before heading to the surface. Rarely did a bird lose a fish after capture (~3%) and it almost always managed to recapture the trout (see Grémillet et al. 2006). After surfacing, birds manipulated the fish so as to swallow it headfirst. Double-crested cormorants are certainly capable of swallowing 'small' fish underwater (M. R. Enstipp pers. obs.). However, in the current study this was only observed in 9 cases out of 275 prey captures and mostly in the 2 largest birds. Handling times at the surface (from surfacing to prey ingestion) were short (mean: 3.8 ± 1.5 s, range: 1 to 12 s). When handling time was calculated as the time from prey capture to prey ingestion (hence, including the time underwater from capture to surfacing), it became largely a function of the depth at which prey was caught.

Most fish that were attacked by a bird seemed to be well aware of the predator early on, as they were actively moving away from it. However, in 18% of all bird attacks a fish remained stationary until the predator was within close range and was captured in 73% of these attacks.

Prey density

The total number of fish inside the dive tank during a trial ranged from 1 to 23, which corresponded to a fish density of 0.005 to 0.117 fish m^{-3} (0.17 to 7.27 g m^{-3}). Of all the parameters investigated, fish density within the dive tank had the strongest effect on cormorant prey-capture behaviour ($F_{8,81} = 33.37$, $p < 0.001$). While cormorants searched on average less than 2 min during a trial when prey density was above 2 g m^{-3} (about 0.04 fish m^{-3} or 7 fish within the tank), search time was greatly increased in trials with lower prey densities (Fig. 2A). Similarly, the time that birds spent submerged at the beginning of a trial before the first fish was encountered was greater in low density trials. Finally, the proportion of dives in a trial during which prey were encountered was low during low density trials, when compared with trials of greater fish density (Fig. 2B). The relationships between fish density and search time as well as prey encounter rate were characterised by a break at a fish density between 2 to 3 g m^{-3} , below which the steepness of the curve changed (Fig. 2). There was also a significant, apparently linear relationship between fish density and prey capture rate (CPUE). High fish densities were associated with greater prey capture rates of cormorants (Fig. 3A). At prey densities below about 2 g m^{-3} , however, the prey capture rate of cormorants was below average and in some trials no fish were caught. While other factors (i.e. fish size, illumination, and fish behaviour) might have confounded the relationship plotted in Fig. 3A, REML analysis showed that none of these factors had a significant influence (for fish size, illumination, and fish behaviour vs. CPUE, $p = 0.73$, 0.74, and 0.85, respectively). However, Fig. 3A was plotted on a per trial basis, so it gives a general view. With respect to fish behaviour, this required classification of trials as either schooling or solitary trials, while in fact both behaviours might have occurred during the same trial. Hence, when looking at individual prey encounters, we found that fish behaviour strongly affected cormorant predatory performance (see below). We also computed prey intake rates by combining the underwater part of the foraging process with the handling time of fish at the surface. Fig. 3B illustrates that the overall foraging process of cormorants feeding on trout resembles the sigmoid type III curve of Holling's model.

Prey size

Body mass and length of the trout ranged from 23 to 108 g and 15.5 to 25 cm, respectively. Within the size range of trout that we investigated, there was no

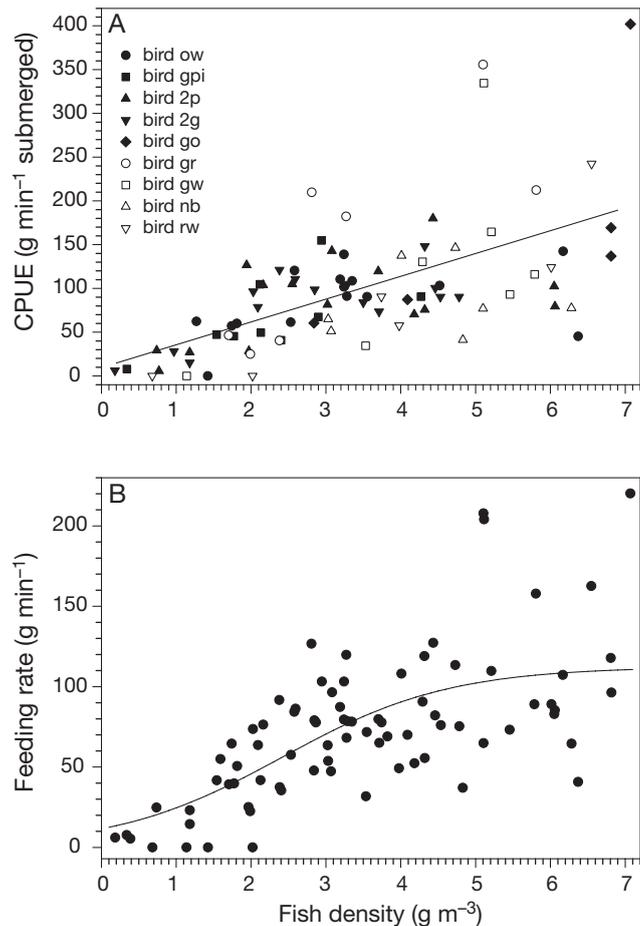


Fig. 3. Prey capture rate (CPUE) and feeding rate of double-crested cormorants versus fish density ($N = 9$ birds, $n = 82$ trials). (A) CPUE increased significantly with an increase in fish density and was best described by $y = 26.04x + 9.6$, where y is CPUE and x is fish density ($F = 6.84$, $p < 0.0001$, $r^2 = 0.45$). (B) Feeding rate includes the underwater part of the foraging process as well as the food handling time at the surface. The relationship was best described by $y = \frac{112.32}{1 + e^{-(x-2.42/1.11)}}$, where y is the feeding rate and x is fish density ($F = 30.83$, $p < 0.0001$, $r^2 = 0.44$)

significant effect of fish size on cormorant predatory performance ($F_{8,81} = 0.12$, $p = 0.73$). The likelihood of getting caught was similar for large (mean TL and M_b : 20.2 cm, 66 g) and for small fish (mean TL and M_b : 17.8 cm, 44 g). In trials with a similar mean fish density (3 to 4 g m^{-3} or 0.06 to 0.07 fish m^{-3}), prey capture rates achieved by the birds were comparable for small fish ($115 \pm 67 \text{ g min}^{-1}$ submerged or 2.2 ± 1.2 fish min^{-1} submerged) and large fish ($100 \pm 25 \text{ g min}^{-1}$ submerged or 1.5 ± 0.3 fish min^{-1} submerged). Plotting mean fish mass during these trials against CPUE did not reveal a significant relationship. Pursuits appeared to be more successful in trials with small fish (67 vs. 61% for large fish) but this difference was not found to be significant

($p = 0.95$, $t = 0.07$). Foraging effort, as indicated by the duration of successful pursuits, was similar for both size classes (6.3 vs. 6.8 s for small and large fish respectively; $p = 0.80$, $t = -0.27$).

Light conditions

Light conditions did not limit the predatory performance of cormorants within the illuminance range tested (1.8 to 120 lx at 10 m depth; $F_{8,49} = 0.11$, $p = 0.74$). Cormorants achieved high prey capture rates even under low light conditions (Fig. 4). While we recorded some low CPUE values especially at the lower end of the illuminance scale (Fig. 4), these were also trials with a low fish density ($< 2 \text{ g m}^{-3}$). Removing the effect of fish density on foraging success (i.e. excluding trials with a fish density $< 2 \text{ g m}^{-3}$) shows that light conditions did not have a significant influence on cormorant foraging success.

Fish behaviour

At higher fish densities within the tank, the trout generally schooled. During the first trials of a day, most trout were therefore part of the school. With the decline in fish numbers throughout successive trials, the school eventually disintegrated and trout remained solitary. Hence school size, and perhaps its packing density, declined throughout successive trials. Furthermore, at the beginning of a trial day, the school moved freely within the water column. However, in response

to predator attack, it moved towards the bottom of the tank and typically remained there until trials were terminated. In our REML analysis, we had to classify trials into either schooling or solitary trials, while in fact both behaviours might have occurred during the same trial. Consequently, fish behaviour was found to have no significant effect on cormorant foraging performance, when considering entire trials ($F_{8,81} = 0.04$, $p = 0.85$). However, when investigating individual prey encounters, the schooling behaviour of the trout (trout schooled in 67% of all trials) had a marked effect on the predatory performance of the cormorants. In 55.8% of all pursuits initiated in 82 trials, birds targeted individual fish that were not part of a school. Of these pursuits 70.8 \pm 22.1% were successful. Of all pursuits recorded 44.2% were directed towards a school. However, the success rate of these pursuits was significantly lower, with only 40.5 \pm 14.5% of pursuits culminating in prey capture ($p = 0.003$, $t = -4.14$). A similar picture emerged when we looked at the prey capture success of cormorants on a per dive basis. Cormorants succeeded in 86.9 \pm 12.9% of dives during which prey was encountered and pursued when solitary prey was targeted, but prey capture success was reduced to 63.3 \pm 20.2% when the target was part of a school ($p = 0.002$, $t = -4.72$). Besides reducing predator success rate, schooling also significantly increased the amount of time birds had to spend in prey pursuit in order to succeed. Birds spent on average 5.2 \pm 1.4 s in pursuit when successfully attacking a solitary fish. In contrast, average pursuit duration was 10.2 \pm 2.9 s, when a fish that was part of a school was attacked and captured ($p < 0.001$, $t = -5.78$). In a few cases we observed birds seemingly ignoring a school close to the surface, diving to the bottom of the 10 m tank instead, where a few solitary fish were present.

DISCUSSION

Our study investigated the effects of various factors on the prey-capture performance of an avian pursuit diver. We found that cormorant foraging success was strongly influenced by prey density. The prey capture rate of cormorants increased linearly with an increase in prey density (Fig. 3A). Fish behaviour also affected cormorant foraging performance, so that capture success was lower and capture effort higher, when birds targeted schooling rather than solitary trout. The functional link between prey density and cormorant foraging performance established in our study (Fig. 3A) should be incorporated into bioenergetic models and will be essential when trying to estimate minimum requirements for these avian divers within changing marine ecosystems. For example, Enstipp et al. (2006)

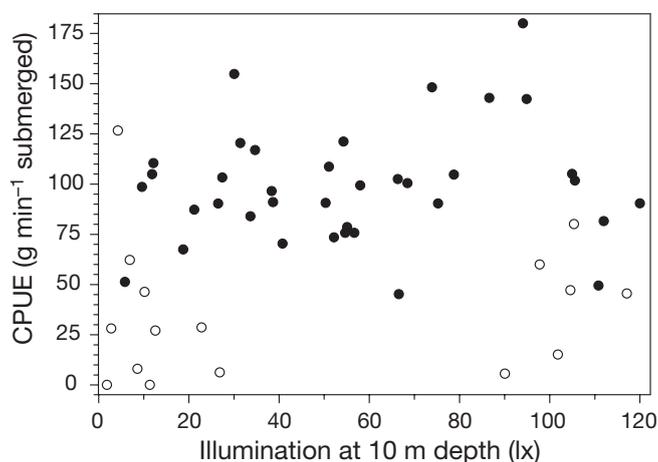


Fig. 4. Prey capture rate of cormorants in relation to illumination measured at the bottom of the tank. Open circles indicate trials when prey density was below 2 g m^{-3} . No clear trend is apparent but cormorants achieved high prey capture rates even at the lower illumination range, indicating that light conditions encountered did not limit their prey capture capabilities. $N = 9$ birds; $n = 54$ trials

compiled an algorithm to calculate the daily food intake for 4 North Sea seabird species from the knowledge of time-activity budgets, energy expenditures and diet, which allowed the calculation of required feeding rates (CPUE). Integrating the relationship between prey density and foraging performance (Fig. 3A) into such an algorithm would allow the calculation of the required overall prey densities for a predator to make ends meet. Such an improved algorithm could then be used to investigate the potential capacity of a predator to buffer a decline in prey availability, when densities will be reduced.

Our experiments were conducted with captive raised birds that foraged within the confined space of a tank on a single prey species. By reducing the complexity that exists in a natural setting, it was possible to investigate quantitative aspects of the predator-prey interactions between cormorants and trout. However, one should keep in mind that our study can only serve as a proxy for the natural situation and our findings should be interpreted in this light. It is a first attempt to investigate how various factors affect the foraging success of an avian pursuit diver. Nevertheless, we believe that it will contribute to our understanding of predator-prey interactions in the marine environment, while we eagerly await detailed investigation in the field. Some of the constraints in our experimental design are as follows: (1) Tank walls clearly restricted the movements of both predator and prey. While tank dimensions were relatively large, it is difficult to judge to what degree the confined space might have worked in favour of the predator. Cormorants captured fish at any position within this tank, at its side (>50%), as well as in its centre, and fish escape movements were directed in the horizontal as well as in the vertical planes. Fish also had the possibility to hide within or behind structures at the bottom of the tank. Hence, we believe that we minimised the effects of a confined space on predator-prey interactions the best we could within the constraints of our set-up. (2) At low fish numbers within the tank, trout did not school and, hence, lost their natural means of predator defence. Consequently, they might have been stressed and, therefore, more susceptible to predator attack. However, even at high densities some trout remained solitary and did not join the school, while they generally made effective use of the shelter provided at the tank bottom. (3) Both trout and cormorants were handled before experimentation and this might have altered their behaviour. However, trout were given at least 2 h to recover from handling before trials started and seemed to behave normally. Cormorants started to dive and forage on trout immediately after introduction to the dive tank, which should indicate that any handling effect was minimal.

Prey density

How do the prey densities we used in our study compare with prey abundances that birds would encounter in the wild? Abundance estimates for fish species not commercially exploited by humans are rare. If we express the fish densities in our study on a m^{-2} basis (the typical unit for abundance estimates), then birds dived in water with fish densities of between 0 and 70 g m^{-2} , which corresponds to 0 to 2.1 trout m^{-2} . Grémillet et al. (2004) estimated the abundance of benthic fish in a foraging area frequented by great cormorants in Greenland to be $0.09 \text{ prey items m}^{-2}$. This was considered to be rather low and estimates of between 0.5 and 2.3 fish m^{-2} are more typical for comparable habitats throughout Europe (see Grémillet et al. 2004). Hence, the fish densities encountered by the cormorants in our study might be a good approximation of the natural situation within coastal, temperate habitats.

Prey density strongly affected the foraging behaviour and success of double-crested cormorants. While a decline in fish density increased the time cormorants spent searching during a trial (Fig. 2A), it decreased both prey encounter rate (Fig. 2B) and prey capture rate (Fig. 3A). In all cases the effect was most noticeable below a fish density of $2 \text{ to } 3 \text{ g m}^{-3}$, when cormorant foraging performance was significantly altered. Hence, $2 \text{ to } 3 \text{ g m}^{-3}$ might represent a threshold density below which sustainable foraging in cormorants is compromised. If such a threshold density exists in a natural situation, it could have important consequences for wild birds confronted with a decline in food abundance, when density levels will be reduced (see Entstipp et al. 2006). At low fish densities birds will be forced to increase foraging effort, elevating energetic requirements. If other prey types are present in sufficient numbers, birds might be able to switch diet. However, the capacity of birds to buffer food decline will ultimately be limited by the amount of food available within a system and the rates at which food can be acquired (Entstipp et al. 2006). Hence, cormorants might not be able to achieve sufficiently high feeding rates at the lower end of fish densities tested in our study.

However, it should be noted that individual differences in the predator avoidance behaviour of the fish may have contributed to the observed shift in predator performance. (1) An intrinsic difference between fish in their ability to avoid being caught by a predator might exist. At the beginning of a trial day fish density was high and gradually decreased throughout successive trials, as birds removed fish. Birds might have preferentially removed fish that were easy to catch, leaving the harder to catch individuals for the later, low density trials. (2) The ability of a fish to avoid a

predator might improve through repeated exposure to a predator. Hence, fish in the later low density trials, could have been more experienced than in the early, high density trials of that day. Wood & Hand (1985) reported that juvenile coho salmon *Oncorhynchus kisutch* with previous predator exposure were captured less frequently by common mergansers *Mergus merganser* than individuals without previous exposure. In our trials trout clearly responded to repeated predator attack. After initial introduction into the tank most trout joined a school that was roaming freely throughout the water column. In a first response to being attacked, the school moved to the bottom of the tank, forcing the predator to dive deeper. Predator attack also often resulted in the temporary breakup of a school into smaller groups, but the school usually reformed immediately afterwards. As fish numbers declined throughout the trials, the school eventually disintegrated and fish sought cover at the bottom. Hence, while birds could probably detect fish easily during the early, high density trials, when fish roamed the water column, they had to search more intensely during the later, low density trials, when fish were hiding. Nevertheless, birds were often successful in locating and capturing fish that were hiding within diverse structures at the bottom.

Few studies have investigated the effect of prey density on the foraging success of avian divers. Two studies investigated the foraging behaviour of *Mergus merganser*; Wood & Hand (1985) and great crested grebes *Podiceps cristatus* (Ulenaers et al. 1992) but both were restricted to shallow ponds or streams. Both studies found a significant increase in prey capture rate with an increase in fish density. Wood & Hand (1985) reported a success rate for mergansers during pursuits initiated from the surface of about 36%. This is well below the overall success rate of pursuits initiated by cormorants in our study (58%). Analysis in the studies on mergansers and grebes was restricted to surface observations, so that few conclusions can be drawn about the underwater behaviour of those species. Capture success in those studies is expressed as the proportion of successful dives, based on the observation of prey handling at the surface. Hence, no information on the frequency of prey encounter, nor the frequency and outcome of predator attacks can be obtained from these studies. The reported proportion of successful dives for avian predators is consequently low with 3.1% for great crested grebes (Ulenaers et al. 1992) and between 3 to 8% for little grebes *Tachybaptus ruficollis* foraging in 1 to 2.5 m deep water (Fox 1994). In our study 51% of all dives conducted by the cormorants ended in the capture and ingestion of a trout, while 78% of all dives during which prey was encountered and pursued were suc-

cessful. Prey densities in the study by Ulenaers et al. (1992) ranged between 0.1 and 2.09 fish m⁻² or 8 and 58 g m⁻² for roach/rudd. These density values are similar to our study, while effective fish density was probably lower in our study because of the depth factor. Hence, density cannot explain the observed difference in prey-capture success between grebes and cormorants. It might be that the prey capture capabilities of cormorants are exceptional among avian divers that have been investigated so far. Grémillet et al. (2001) reported CPUE values for great cormorants foraging in Greenland during winter of up to 60 g fish min⁻¹ submerged. At the highest fish density tested in our study (7 g m⁻³) cormorants reached CPUE values in the order of 190 g fish min⁻¹ underwater. This density was most likely considerably higher than that typically encountered by cormorants in Greenland (see Grémillet et al. 2004). However, it also suggests that cormorants might be able to achieve a higher foraging yield than reported in field studies, if fish densities are sufficiently high.

The underwater part of the foraging process in cormorants showed a linear relationship with fish density (Fig. 3A), and, hence, resembles a type I curve in Holling's model (Holling 1959). However, the relationship between overall feeding rate (including the handling time at the surface) and fish density (Fig. 3B) was characterized by a sigmoid-shaped curve (type III curve in Holling's model). This would indicate that at higher fish densities prey handling limits the further increase in feeding rate in double-crested cormorants. A levelling off at higher prey densities has also been reported for other piscivorous birds, albeit in a hyperbolic shaped curve (type II curve in Holling's model, Wood & Hand 1985, Draulans 1987, Ulenaers et al. 1992).

Prey size

Size of trout did not affect cormorant foraging behaviour in our study. Prey capture rates were similar for both size classes (small and large) and so were the durations of successful pursuits, indicating that capture effort was comparable. In contrast, Ulenaers et al. (1992) found a significant effect of fish size on the foraging behaviour of great crested grebes. In their study, the proportion of successful dives increased as fish mass decreased, while the duration of successful dives increased with fish mass (range: 8 to 40 g for roach/rudd), suggesting a longer underwater handling time for larger fish. The size range of prey presented to the cormorants in our study falls well within the typical size range of prey exploited by double-crested cormorants in the wild (Derby & Lovvorn 1997). While

rainbow trout of the size range offered in our study did not challenge cormorant prey-capture capabilities, this could be different for other prey species exploited by the cormorants.

Light conditions

The light conditions encountered by cormorants in our study did not limit their prey capture capabilities. Birds achieved high capture rates even at light levels below 5 lx (measured at 10 m depth; Fig. 4). It could be argued that light levels were not uniform throughout our dive tank, facilitating prey capture near the top where more light was available. However, cormorants predominantly captured trout near the bottom of the tank during these trials, where light levels were lowest. Unfortunately, we were unable to run trials at even lower light levels and it is conceivable that light levels below the ones tested in our study would soon have limited cormorant predatory performance. Nevertheless, the range of light conditions tested in our study compares well with conditions naturally encountered by avian divers during foraging. Wanless et al. (1999) recorded light levels that European shags *Phalacrocorax aristotelis* and South Georgian shags *P. georgianus* encountered during diurnal foraging. Illumination at depth ranged from 0.5 to 100 lx for the deeper diving South Georgian shags (mean depth: 3 to 73 m), while European shags (mean depth: 8 to 35 m) dived at light levels of between 7.9 to 100 lx. Both species feed predominantly near the sea bottom, hence, prey search and presumably capture must have taken place at the lower range of light levels encountered. Recently Grémillet et al. (2005) found that great cormorants wintering in Greenland conducted 46% of their foraging dives during the polar night in the dark (<1 lx at the surface). Hence, they suggested that cormorants might switch from visual cues to tactile and/or acoustic cues to capture their prey at these low light conditions. While this might be a realistic scenario for capturing benthic prey (e.g. sculpins), it seems highly unlikely for pelagic/schooling prey like the trout in our study. In little penguins *Eudyptula minor* foraging activity within a shallow dive tank (1.3 m depth) declined with decreasing light levels (Cannell & Cullen 1998). As light levels decreased, penguins reduced the time spent searching for live fish, while pursuits were also initiated less frequently. No fish were caught at light levels below $0.01 \mu\text{e m}^{-2} \text{s}^{-1}$ (equivalent to about 0.6 lx; using the conversion factor given by Cannel & Cullen 1998: $1000 \text{ lx} = 16.5 \mu\text{e m}^{-2} \text{s}^{-1}$). The visual resolution of great cormorants *P. carbo* underwater is exceptionally good (Strod et al. 2004). It is better than

in most fishes and marine mammals, despite the challenge of living in 2 different media (air/water) that require compensatory mechanisms. However, water turbidity strongly affects the visual environment of cormorants underwater and decreases image resolution (Strod et al. 2004). In this context it is interesting to note that great cormorants at Lake IJsselmeer in Holland switched from a solitary foraging habit to mass fishing as visibility declined during the 1970s (van Eerden & Voslamber 1995). However, the effects of very low light levels and turbidity on the prey-capture performance of avian divers remain to be investigated.

Fish behaviour

Schooling is an important anti-predator behaviour in many fish species. It provides protection from predators through a number of mechanisms, such as early predator warning, the encounter-dilution effect, and the predator confusion effect (see Pitcher & Parrish 1993 for review). Overall vigilance will be increased in schools, allowing earlier detection of a predator, increasing the likelihood of a successful escape. The likelihood for an individual of being detected and attacked is diluted in a school and decreases with increasing group size. An attacking predator will be confused because of the many moving targets within a school that cause a sensory overload, making it difficult for the predator to single out and track an individual prey. The effectiveness of these mechanisms has been demonstrated in experimental studies. Neill & Cullen (1974) for example showed that the success rate of cephalopod and fish predators attacking schooling fish decreased significantly with an increase in group size. Attacks were much more likely to be successful if single prey was targeted. Furthermore, attacks on larger schools lasted longer. Similarly, Krause & Godin (1995) found that hunting success of cichlid predators attacking free-swimming guppy schools decreased significantly with increasing school size. Zheng et al. (2005) developed a model to investigate the most efficient behaviour pattern for individuals within a school to avoid being caught by a predator. They found that in schools of increasing size the confusion effect resulted in an increase in the number of attacks before capture. The predator also changed its target more often in larger schools, illustrating how difficult it was for the predator to continuously pursue a single fish within the school. Hence, the significant decrease in foraging success and the significant increase in pursuit duration that we observed when cormorants targeted schooling trout rather than individual trout is in agreement with the findings of the above studies on fish predators.

Cormorants attacking a school deployed a strategy similar to the anti-confusion tactics described by Zheng et al. (2005). They either charged into a school, splitting the school into smaller groups and/or they isolated a single fish from the group, which was then pursued and in most cases captured. Birds were also more likely to switch the target when they attacked a school rather than a single fish. Of all bird attacks, 18% were directed towards an individual that remained stationary until the predator was within close range, rather than trying to maintain the distance to the predator. Since in most cases fish seemed to be well aware of the predator, this behaviour might represent a different strategy, whereby a fish might have tried to rely on camouflage rather than actively swimming away. This behaviour was most often observed when fish were near the bottom of the tank, where added structural elements could have provided some shelter from the predator. However, 73% of these attacks resulted in prey capture, while the average success for all pursuits was only 58%, which should question the effectiveness of this strategy. Alternatively, these individuals might have been stressed after losing their natural mean of predator defence, schooling.

In conclusion, our experimental investigation illustrates the importance of a variety of factors in conditioning the fine scale foraging behaviour of an avian diver. The prey capture rates of cormorants and their modulation by various factors reported in this study should be incorporated into feeding models of piscivorous diving birds (see Lovvorn et al. 2001), which in turn might help to understand predator requirements in a changing environment.

Acknowledgements. Research was conducted and funded within the framework of the European Commission project Interactions between the marine environment, predators and prey: implications for sustainable sandeel fisheries (IMPRESS; QRRS 2000-30864). Financial support was also provided by a 'Discovery grant' and equipment grants from NSERC to D.R.J. The British Columbia Ministry of Environment granted holding permits for the double-crested cormorants. A. Vanderhorst and S. Gopaul (UBC Animal Care) provided support in caring for the birds. Thanks to B. Gillespie and D. Brandies (UBC Zoology Mechanical Workshop) for technical help and to K. Scheer (Fraser Valley Trout Hatchery) for generously providing live rainbow trout. T. Hoeg was indispensable in setting up the underwater camera system and generously donated knowledge, expertise and time. M. Grantham helped during all stages. Thanks to J. Gosline and R. Liley (UBC Zoology) for access to equipment and for tolerating the takeover of the fish holding tanks. G. Peters (Earth&Ocean Technologies) kindly provided the GeoLT data logger and L. Toolsy helped during the long hours of video analysis. J.-P. Robin and J.-Y. Georges provided statistical advice. Thanks to G. Weingartner, G. Ruxton and R. Liley for reviewing an earlier version of this manuscript and to 3 anonymous referees for their constructive comments.

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Editorial responsibility: Rory Wilson (Contributing Editor), Swansea, UK

*Submitted: March 24, 2006; Accepted: July 20, 2006
Proofs received from author(s): February 5, 2007*