Predator size, prey size and threshold food densities of diving ducks: does a common prey base support fewer large animals?

Samantha E. Richman* and James R. Lovvorn

Department of Zoology, University of Wyoming, Laramie, WY 82071, USA

Summary

1. Allometry predicts that a given habitat area or common prey biomass supports fewer numbers of larger than smaller predators; however, birds from related taxa or the same feeding guild often deviate from this pattern. In particular, foraging costs of birds may differ among locomotor modes, while intake rates vary with accessibility, handling times and energy content of different-sized prey. Such mechanisms might affect threshold prey densities needed for energy balance, and thus relative numbers of different-sized predators in habitats with varying prey patches.

2. We compared the foraging profitability (energy gain minus cost) of two diving ducks: smaller lesser scaup (*Aythya affinis*, 450–1090 g) and larger white-winged scoters (*Melanitta fusca*, 950–1800 g). Calculations were based on past measurements of dive costs with respirometry, and of intake rates of a common bivalve prey ranging in size, energy content and burial depth in sediments.

3. For scaup feeding on small prey < 12 mm long, all clams buried deeper than 5 cm were unprofitable at realistic prey densities. For clams buried in the top 5 cm, the profitability threshold decreased from 216 to 34 clams m^{-2} as energy content increased from 50 to 300 J $clam^{-1}$.

4. For larger scoters feeding on larger prey 18–24 mm long, foraging was profitable for clams buried deeper than 5 cm, with a threshold density of 147 m^{-2} for clams containing 380 J $clam^{-1}$. For clams < 5 cm deep, the threshold density decreased from 86 to 36 clams m^{-2} as energy content increased from 380 to 850 J $clam^{-1}$. If scoters decreased dive costs by swimming with wings as well as feet (not an option for scaup), threshold prey densities were 11–12% lower.

5. Our results show that threshold densities of total prey numbers for different-sized ducks depend on prey size structure and depth in the sediments. Thus, heterogeneity in disturbance regimes and prey population dynamics can create a mosaic of patches favouring large or small predators. Whether a given area or total prey biomass will support greater numbers of larger or smaller predators will vary with these effects.

Key-words: bivalve burial depth, body size scaling, carrying capacity, functional response, predator coexistence

Introduction

Body size is often invoked as a major force structuring biotic communities, and as a key determinant of predator habitat requirements. Efforts to protect adequate habitat are concerned with predicting the densities of animals of different sizes (Silva & Downing 1994; Jetz *et al.* 2004; Damuth 2007). Allometry predicts that a given habitat area or prey biomass supports fewer numbers of larger than smaller animals (Damuth 1981; Carbone & Gittleman 2002). However, birds from related taxa or particular foraging guild often deviate from this pattern, with larger species having higher densities than smaller ones (Damuth 1991; Nee *et al.* 1991; Blackburn *et al.* 1994; Cotgreave 1994). Thus, despite the appeal of using a simple and inexpensive approach, allometry can yield misleading estimates of the extent of habitat required to support birds of different body sizes, and better understanding of mechanisms driving the densities of different species is needed (Juanes 1986).

*Correspondence author. E-mail: cruciger@uwyo.edu

Relative numbers of different-sized predators may ultimately depend on their ability to meet their energy requirements at different levels of prey abundance. In particular, it is important to consider the fractions of prey of different sizes or accessibility that are effectively available to predators of differing body size (Werner 1979; Zwarts & Wanink 1984; Persson 1985; Dickman 1988). Larger species can search larger areas per unit time and eat greater amounts and size ranges of foods (Mittelbach 1981). As a result, larger predators may withstand prey depletion better than smaller predators restricted to smaller food items and thus a lower fraction of total food biomass (Schoener 1974; Gerritsen & Kou 1985; Goudie & Ankney 1986). Conversely, larger body size incurs higher absolute costs for maintenance metabolism and locomotion. Because smaller species have lower absolute energy requirements, they may endure reduced prey availability better than larger species (Persson 1985). Among species that partition the same prey taxa by size (Zwarts & Wanink 1984; de Leeuw 1999), the outcome of these energetic tradeoffs will depend on the size structure of prey, and differences in accessibility, handling time, ingestibility and energy content among prey of different sizes (Zwarts & Wanink 1993). Moreover, varying types of disturbance may create habitat patches with contrasting prey size structures that favour either larger or smaller predators (Eriksson *et al.* 2005).

Differences in foraging profitability (energy gain minus cost) between different-sized predators should alter thresholds of prey density at which energy balance switches from positive to negative. Prey density thresholds below which animals stop feeding and move elsewhere have been observed and explored theoretically for a range of taxa (e.g. Brown 1988), including birds that feed on foods buried in sediments (Nolet, Fuld & van Rijswijk 2006). Such 'giving up densities' may be higher than the threshold of energy balance (Nolet *et al.* 2002), perhaps depending on expected net profit of searching for better patches (Bernstein, Kacelnik & Krebs 1988). However, in one case for a diving duck, the density of maximum depletion determined by exclosure experiments (Sponberg & Lodge 2005) corresponded well with that predicted from a model of energy balance (Lovvorn & Gillingham 1996).

Scoters and scaup are diving ducks that coexist at a number of wintering and migration areas, where they feed mainly on benthic invertebrates (Vermeer & Levings 1977; Nilsson 1980; Perry 1987; Goudie & Ankney 1988; Accurso 1992; Anderson, Lovvorn & Wilson 2008). For waterfowl, winter is often a time of food limitation that promotes niche partitioning (DuBowy 1988; Goudie & Ankney 1988; but see Nudds & Wickett 1994), and the intake rates of scoters and scaup at different prey densities differ according to prey size and burial depth in sediments (Richman & Lovvorn 2003, 2004). Although other taxa (polychaetes, crustaceans, herring spawn) are sometimes important foods, bivalves commonly dominate the diets of these ducks in soft-bottom habitats. Of the species of soft-bottom clams eaten by both scaup and scoters in different areas, some (e.g. *Corbula, Gemma, Mulinia*) are always small and near the sediment surface, whereas others (e.g. *Macoma, Mya, Nuttallia, Scrobicularia*) can grow large and bury more deeply as they grow (cf. Chambers & Milne 1975; Hines & Comtois 1985; Zwarts & Wanink 1989, 1993; Poulton 2001; Lewis, Esler & Boyd 2007). Because of large changes in nutrient stores of seasonally reproducing bivalves, and varying ecological conditions among areas, species such as the holarctic *Macoma balthica* Linnaeus can also vary greatly in energy content for the same shell length (see Materials and methods).

Also critical to models of foraging profitability are measures of the metabolic costs of foraging, which include both locomotion and thermoregulation underwater. For diving birds, mass-specific work against buoyancy and hydrodynamic drag, and heat loss to cold water, decrease with increasing body size (Lovvorn & Jones 1991; Lovvorn, Jones & Blake 1991; Lovvorn 2006). Larger animals can also store more oxygen and have lower mass-specific metabolic rates (Butler & Jones 1982). In addition, the larger scoters can reduce dive costs by altering their locomotor mode: lesser and greater scaup (*Aythya affinis* Eyton, *Aythya marila* Linnaeus) swim only with their feet, whereas surf and whitewinged scoters (*Melanitta perspicillata* Linnaeus, *Melanitta fusca* Linnaeus) can swim with feet only or with wings in addition to feet. For dives 2 m deep, using wings as well as feet reduced costs of descent in white-winged scoters by 34% (Richman & Lovvorn 2008).

For sympatric diving ducks with similar diets and feeding methods, important questions are:

1. How do body size and locomotor mode affect foraging profitability for prey of different densities, sizes, and depths in the sediments?
2. Below what prey density thresholds are these different-sized ducks unable to meet their energy requirements?

These questions are critical to understanding the relative roles of these important predators in food webs, as well as delineating viable habitat and predicting the extent of habitat needed to support both species. To address these problems, we combined experimental measurements of dive costs and intake rates for smaller lesser scaup (LESC, 450–1090 g) and larger white-winged scoters (WWSC, 950–1800 g). We also calculated effects of seasonal and among-site variations in energy content of bivalve prey of the same size. Measurements were taken from previous studies under the same experimental conditions for scaup (Richman & Lovvorn 2004; Kaseloo & Lovvorn 2005) and scoters (Richman & Lovvorn 2003, 2008). Although prey patch structure and associated search costs can also be important to energy balance and threshold food densities (Lovvorn & Gillingham 1996), analyses here are for birds that have already located patches of uniform prey density and quality. We also evaluated effects of shifts in prey size structure and depth distribution on the relative suitability of different prey patches to larger and smaller ducks.

Materials and methods

ENERGY INTAKE

Energy intake (EI, J dive^{-1}) was calculated as

$$EI = I_{ij} \times AE_N \times EC \times t_{bott}, \qquad \text{eqn 1}$$

where I_{ij} is the intake rate (number of prey items consumed per second spent foraging at the bottom) for different prey sizes (i, mm) and depths in the sediments (j, cm), AE_N is the assimilation efficiency or fraction of ingested energy absorbed by the gut corrected for nitrogen retention (no units), EC is the energy content (J) per whole clam and t_{bott} is the average time (s) spent foraging at the bottom.

We previously measured intake rates (I_{ij}) for LESC (Richman & Lovvorn 2004) and WWSC (Richman & Lovvorn 2003) freely diving in a large concrete dive tank ($2 \times 5 \times 2$ m deep) at the Delta Waterfowl and Wetlands Research Station, Manitoba, Canada (hereafter referred to as Delta). The birds were trained to feed in a sand-filled tray (0·5 m wide × 1 m long × 9 cm deep) at the bottom of the tank. LESC fed on prey < 12 mm long at two burial depths in the sand (3 and 6 cm) at 10 prey densities from 50 to 4000 prey m^{-2}. WWSC fed on clams 18–24 mm long buried at 4 and 7 cm depths at seven prey densities from 50 to 1600 prey m^{-2}.

The intake rate model is $I = aX/(b + X)$, where I is the number of prey consumed per second foraging at the bottom, X is the number of prey m^{-2}, a is the handling time coefficient or the maximum rate at which prey items can be consumed regardless of prey density, and b is the search time coefficient or the prey density at an intake rate of 0·5a (Lovvorn & Gillingham 1996). We used intake rate curves reported by Richman & Lovvorn (2004) for scaup foraging on clams < 12 mm long that were buried in the sediments at either 3 cm depth, $I_{12mm, 3cm} = 3·75X/(3260 + X)$, or 6 cm depth, $I_{12mm, 6cm} = 0·66X/(4018 + X)$. For scoters, we used intake rate curves of $I_{18mm, 4cm} = 0·75X/(591 + X)$ for clams 18–24 mm long at 4 cm sediment depth, and $I_{18mm, 7cm} = 0·54X/(682 + X)$ for clams 18–24 mm long at 7 cm sediment depth (Richman & Lovvorn 2003).

Prey size ranges for each duck species corresponded to those found in diet studies of scaup in San Francisco Bay, USA (S.L. Wainwright-De La Cruz, unpublished data) and of scoters in Chesapeake Bay, USA (Perry *et al.* 2007). Field studies have indicated that even larger diving ducks generally restrict their digging for prey to the top 10 cm of sediments (Lovvorn 1989). Within that range, our experimental depths corresponded to approximate depths of *M. balthica* of different shell lengths during winter in the Netherlands (Zwarts & Wanink 1989; Zwarts *et al.* 1994) and San Francisco Bay (Poulton, Lovvorn & Takekawa 2002, 2004). Although the larger scoters can ingest smaller as well as larger clams, available data suggest that diving ducks develop a strong search image for the size classes of bivalves that are most profitable, while ignoring other size classes that they eat elsewhere (Lovvorn *et al.* 2003). Because larger clams were more profitable for scoters (see Results), we assumed that they focused on the larger prey that are not eaten by scaup. However, we acknowledge that scoters can and do eat smaller prey.

Assimilation efficiency corrected for nitrogen retention (AE$_N$) for scaup consuming *M. balthica* was 63% (Richman & Lovvorn 2004). No published data exist on AE$_N$ of clams by scoters, but the value for common eiders (*Somateria mollissima*) consuming *Macoma calcarea* was 75% (Richman & Lovvorn 2003). We varied AE$_N$ in our calculations between 63%, 70% and 75%, and found that AE$_N$ had little effect (< 10%) on estimates of profitability. We therefore used an AE$_N$ of 70% for both predator species, and for all prey sizes.

Energy content (EC, J clam^{-1}) of *M. balthica* varies widely among seasons, years and locations. Diving ducks consume whole clams, so energy values presented here are for entire clams including shells. In San Francisco Bay on the West Coast of the USA, EC of *M. balthica* in winter was 50 J clam^{-1} for specimens 6–12 mm long and 380 J clam^{-1} for specimens 18–24 mm long (Richman & Lovvorn 2004). However, in the Dutch Wadden Sea, EC for *M. balthica* was 213 J for clams 6–12 mm long and 849 J for clams 18–24 mm long (Zwarts & Wanink 1993). In the Ythan Estuary, Scotland, EC of *M. balthica* varied substantially with the reproductive cycle of breeding adults. In February before spawning, *M. balthica* 18–24 mm long contained an average of 2041 J clam^{-1}, declining to an average of 1318 J clam^{-1} after spawning in April. *Macoma balthica* 6–12 mm long declined only from 222 to 199 J clam^{-1} over the same period, but reached 332 J clam^{-1} by November (Chambers & Milne 1975). Given this variability, we used a range of clam energy values in our calculations to assess the importance of that variable to gross energy intake. For clams < 12 mm long (scaup), we used 50, 150 and 300 J clam^{-1}; for clams 18–24 mm long (scoters), we used 380, 600 and 850 J clam^{-1}.

COST OF DIVING

Energy cost per dive (C, Joules) was measured previously for LESC (Kaseloo & Lovvorn 2005) and WWSC (Richman & Lovvorn 2008) diving to 2 m in water at 8–9 °C. The dive tank for respirometry studies at the Red Buttes Environmental Biology Laboratory, University of Wyoming (hereafter Red Buttes), had the same depth as the Delta tank used for foraging measurements, but had substantially shorter length and width (1·55 m long × 0·73 m wide vs. 5 m long × 2 m wide). Perhaps as a result, the durations of bottom foraging and of overall dives were greater in the Delta tank.

Methods used to calculate metabolic costs of diving are explained in detail by Richman & Lovvorn (2008). Briefly, the rate of oxygen consumption was determined by the fractional equivalent method of Withers (1977) and Bartholomew, Vleck & Vleck (1981). Total cost of diving was measured from the onset of the first dive in a bout until the bird returned to resting metabolism following the dive bout (including dives, pauses between dives and subsequent period of recovery at the surface). We then subtracted the costs of surface behaviours (swimming or preening, measured during periods of no diving) and divided the remainder by the time spent underwater. Values of metabolic power for different dive phases (descent, bottom and ascent) were calculated for scaup by assuming that the cost of passive ascent (driven by positive buoyancy) was equal to the cost of resting on water at that temperature; we then subtracted the ascent cost, and the descent cost for dives with no time spent at the bottom, from total cost to yield cost at the bottom (Kaseloo & Lovvorn 2005). For scoters, the metabolic power of each phase for dives by feet only and by wings + feet was partitioned based on the fraction of total work during descent and bottom foraging for scaup (Richman & Lovvorn 2008).

Because profitability (energy gain minus cost) depends strongly on the duration of bottom foraging, which affects both total food intake and total dive cost, we adjusted the dive cost for the different tank. To adjust the cost of diving (C_{adj}) in the Red Buttes tank to longer bottom times during foraging experiments in the Delta tank, we multiplied the metabolic power (MP, mL O$_2$ s^{-1}) for different dive phases in the Red Buttes tank (from Table 1 in Kaseloo & Lovvorn 2005 for scaup, from Table 2 in Richman & Lovvorn 2008 for scoters) by the duration of each phase in the Delta tank (Tables 1 and 2):

Table 1. Means ± SEM of dive-phase durations (s) in the Delta ($n = 4$) and Red Buttes ($n = 4$) tanks, and of metabolic power (MP, mL O_2 s^{-1}) in the Red Buttes tank, for lesser scaup diving to 2 m depth in water 8–9 °C

| Dive phase | Dive-phase duration (s) | | MP (mL O_2 s^{-1}) |
	Delta	Red Buttes	
Descent	2·7 ± 0·1	3·8 ± 0·2	0·288
Bottom	9·6 ± 1·1	5·6 ± 0·7	0·279
Ascent	2·7 ± 0·1	3·0 ± 0·2	0·160
Total	14·8 ± 1·2	12·4 ± 0·8	0·250

Metabolic power and dive-phase durations at Red Buttes are from the study of Kaseloo & Lovvorn (2005). Costs include resting metabolism.

$$C_{adj} = (MP_{desc} \times t_{desc}) + (MP_{bott} \times t_{bott}) + (MP_{asc} \times t_{asc}), \qquad \text{eqn 2}$$

where MP is the metabolic power and t is the duration (s) for descent (MP_{desc}, t_{desc}), bottom (MP_{bott}, t_{bott}) and ascent (MP_{asc}, t_{asc}) phases of a dive. The adjusted cost of diving in the Delta tank (C_{adj}) was converted to Joules by a value of 20·1 J (mL O_2)$^{-1}$, based on a measured respiratory quotient of 0·8 for fed birds (Schmidt-Nielsen 1997; Kaseloo & Lovvorn 2005; Richman & Lovvorn 2008). For WWSC, we calculated the cost of dives separately when descent was propelled by feet only or by wings as well as feet (Richman & Lovvorn 2008).

FORAGING PROFITABILITY

To assess effects of both energy intake and foraging costs for ducks of different body size, we calculated the foraging profitability (FP, J dive^{-1}) for LESC and WWSC foraging on clams of differing size, energy content and depth in the sediments. We calculated FP as

$$FP = EI_{ij} - C_{adj}, \qquad \text{eqn 3}$$

where EI_{ij} is the assimilated energy intake rate (J dive^{-1}) as a function of prey density for a given prey size (i) and depth in the sediments (j) (see Energy intake section above for calculation), and C_{adj} is the cost of diving to 2 m (J dive^{-1}) adjusted to the cost and duration of different dive phases in the Delta tank. Assimilated energy intake rates (EI_{ij}, J dive^{-1}) for each prey density were generated from the functional responses for the different prey size ranges (< 12 mm for scaup and 18–24 mm for scoters), three prey energy values, assimilation efficiency and time spent foraging at the bottom of the tank. Result-

ing values were fitted with Michaelis–Menten equations (Marquardt method, PROC NLIN, SAS Institute 1987). Foraging profitability curves (FP, J dive^{-1}) for each duck species were calculated by subtracting the cost of diving (J dive^{-1}) from the curve of assimilated energy intake rate for each prey density, size and energy content. Threshold food densities were estimated as prey densities at which foraging profitability equalled zero. For simplicity, we discuss foraging on clams buried either < 5 or > 5 cm in the sediments for functional responses measured for scaup (3 and 6 cm) and scoters (4 and 7 cm).

EFFECTS OF PREY ACCESSIBILITY

Periodic disturbances of varying scales, including salinity changes, sediment deposition or scouring, impacts of predators, or other effects on mortality and recruitment, can cause substantial variations in the size structure and associated depth distributions of clams (Nichols & Thompson 1985; Emerson & Grant 1991; Hiddink *et al.* 2002). Because prey communities include an assortment of sizes and depths in the sediments, we calculated the total prey density required to meet the profitability threshold for a specific size–depth class. We then evaluated the net effects of a shift in prey size structure and depth distribution on the total prey density required to meet energy balance.

In the top 10 cm of sediments where most foraging by diving ducks occurs (Lovvorn 1989), the winter depth distribution of different sizes of *M. balthica* in the Dutch Wadden Sea (Zwarts & Wanink 1989) resembled that in San Francisco Bay (Vassallo 1971; Poulton 2001) and the Fraser River Estuary, British Columbia (McGreer 1983). Based on these studies, we assumed for *M. balthica* that: (i) 50% of all clams present in winter are in sediments < 5 cm deep, of which 60% are < 15 mm long (available to scaup) and 40% are > 15 mm long (available to scoters); and (ii) all clams > 5 cm deep in the sediments are > 15 mm long (available only to scoters).

According to the above depth distribution by size, of the clams in the top 5 cm of sediments, 30% of all clams were < 15 mm long, 20% of all clams were > 15 mm long, and 50% were > 15 mm long and buried > 5 cm deep. From these percentages, we calculated the number of clams m^{-2} in different size–depth classes as a function of the total clam density of all size–depth classes combined. Using the profitability thresholds for scaup and scoters feeding on specific size–depth classes for the highest energy clams (300 J clam^{-1} for scaup and 850 J clam^{-1} for scoters, see Results), we determined profitability thresholds for both predators in terms of total clam densities.

To evaluate effects of changing prey size structure on the profitability of foraging by scaup and scoters, we then assumed that under

Table 2. Means ± SEM of dive-phase durations (s) in the Delta ($n = 4$) and Red Buttes ($n = 4$) tanks, and of metabolic power (MP, mL O_2 s^{-1}) in the Red Buttes tank, for white-winged scoters diving to 2 m depth using feet only or wings as well as feet in water 8–9 °C

| Dive phase | Dive-phase duration (s) | | | | |
| | Feet only | | | Wings + feet | |
	Delta	Red Buttes	MP (mL O_2 s^{-1})	Red Buttes	MP (mL O_2 s^{-1})
Descent	4·4 ± 0·1	6·1 ± 0·4	1·011	5·3 ± 0·1	0·665
Bottom	12·7 ± 2·7	7·8 ± 0·7	0·730	12·4 ± 2·4	0·730
Ascent	3·6 ± 0·3	4·2 ± 0·3	0·320 ± 0·018	4·4 ± 0·4	0·320 ± 0·018
Total	20·5 ± 2·8	18·0 ± 1·3	0·734 ± 0·064	22·2 ± 2·1	0·630 ± 0·129

Metabolic power and dive-phase durations for scoters at Red Buttes are from the study of Richman & Lovvorn (2008); see that paper for method of partitioning MP for descent vs. bottom foraging. Costs include resting metabolism.
Note: We did not measure dive-phase durations for dives by wings + feet at Delta and used the durations of dives using feet only.

conditions of heavy predation or low annual recruitment, 25% (vs. 50%) of all clams were < 5 cm deep, but that depth distributions of different sizes remained the same (see Poulton 2001). Conversely, we assumed that under conditions of high annual recruitment, 75% (vs. 50%) of all clams were buried < 5 cm deep while the depth distributions of different sizes remained the same (see McGreer 1983). For each shift in prey size–depth structure (to 25% or to 75% of clams in the top 5 cm of sediments), we calculated the profitability thresholds of total clam density of all size–depth classes combined for scaup and scoters to assess how such prey shifts might favour scoters vs. scaup.

Results

The adjusted cost of diving (C_{adj}) for scaup (always propelled by feet only) was 78 J dive^{-1} (based on the metabolic power for each dive phase measured in the Red Buttes tank multiplied by phase durations in the Delta tank, data in Table 1). For scoters, C_{adj} for feet-only dives was 299 J dive^{-1} and for dives using wings + feet was 10% lower at 268 J dive^{-1} (calculated from data in Table 2). For scaup foraging on prey < 12 mm long and scoters foraging on prey 18–24 mm long, gross energy intake was limited by handling time (coefficient a) at much higher densities for prey with higher energy content (Table 3). However, increasing depth in the sediments from < 5 to > 5 cm had a more profound influence on intake rates of scaup than for scoters (reduction of 82% vs. 28%, Richman & Lovvorn 2003, 2004). As a result, all clams buried > 5 cm deep in the sediments were unprofitable at realistic prey densities for the smaller scaup. For clams buried < 5 cm deep and < 15 mm long, scaup could forage profitably at lower densities (34 clams m^{-2}) for high-energy prey (300 J clam^{-1}) than for low-energy prey (50 J clam^{-1}, 216 clams m^{-2}) (Table 4, Fig. 1a,c).

Table 3. Fitted parameters of the functional responses of assimilated energy intake (EI, J dive^{-1}) for lesser scaup ($n = 4$) feeding on clams < 12 mm long with energy values of 50, 150 and 300 J clam^{-1} buried 3 and 6 cm in the sediments, and for white-winged scoters ($n = 4$) feeding on clams 18–24 mm long with energy values of 380, 600 and 850 J clam^{-1} at depths of 4 and 7 cm

Energy content (J clam^{-1})	Parameter	Prey depth	
		< 5 cm	> 5 cm
Lesser scaup			
50	a	1260	222
150	a	3782	662
300	a	7564	1324
	b	3260	4018
White-winged scoter			
380	a	2344	1688
600	a	3701	2665
850	a	5243	3775
	b	591	682

The functional response model is EI $= aX(b + X)^{-1}$, where EI is the energy intake per dive (J dive^{-1}), a is the handling time coefficient, X is the number of prey m^{-2} and b is the search time coefficient (see Methods). Values of b are constant for the same prey depth because the same functional response equation for intake was used.

Table 4. Threshold prey densities (clams m^{-2}) for size-specific depth classes for lesser scaup feeding on clams < 12 mm long with energy values of 50, 150 and 300 J clam^{-1} buried at 3 and 6 cm in the sediments, and for white-winged scoters feeding on clams 18–24 mm long with energy values of 380, 600 and 850 J clam^{-1} at depths of 4 and 7 cm

Energy content (J clam^{-1})	Dive type	Prey depth	
		< 5 cm	> 5 cm
Lesser scaup			
50	Feet only	216	2186
150	Feet only	69	538
300	Feet only	34	252
White-winged scoter			
380	Feet only	86	147
	Wings + feet	78	129
600	Feet only	52	86
	Wings + feet	46	76
850	Feet only	36	59
	Wings + feet	32	52

Profitability thresholds were calculated as assimilated energy intake rate (Table 3) minus the cost of diving to 2 m with feet only or wings + feet by scoters (Tables 1 and 2).

For larger scoters that can eat much larger prey (> 18 mm) with higher energy content, foraging was profitable on clams buried > 5 cm deep at much lower prey densities (147 m^{-2}) than for scaup (Table 4, Fig. 1d,e,f). For clams buried < 5 cm in the sediments, increasing energy content from 380 to 850 J clam^{-1} decreased this threshold from 86 to 36 m^{-2}. If scoters swam by wings in addition to feet, threshold densities were 11–12% lower (Table 4, Fig. 1).

Size structure and associated burial depth of prey had strong influence on the total density of all prey above which either scaup or scoters could forage profitably (Fig. 2). If clam recruitment were low and only 25% of all clams were < 5 cm deep (Fig. 2a), the threshold prey density would be 227 clams m^{-2} for scaup and 320 m^{-2} for scoters feeding at depths < 5 cm. These densities are far greater than those typically observed for *M. balthica* in the field, suggesting that scaup could not persist in the habitat at all. Scoters, however, could forage profitably on deeper clams at reasonable total densities > 79 m^{-2} (Fig. 2a). With improved recruitment and 50% of all clams buried < 5 cm deep (Fig. 2b), scaup could persist in the habitat at total clam densities exceeding 113 m^{-2} (Fig. 2b), while scoters could persist at densities as low as 118 m^{-2} if they focused on deeper clams. Under conditions of high recruitment with 75% of all clams in the top 5 cm and 60% being < 15 mm long (see Methods), scaup could forage profitably at low total prey densities (> 76 clams m^{-2}) whereas scoters would require much higher total densities of either shallow (> 120 m^{-2}) or deeper clams (> 236 m^{-2}, Fig. 2c). In the latter case, scaup could persist in the habitat whereas scoters could persist only if there were enough large clams in the top 5 cm. Note that scoters could also eat smaller clams in the top 5 cm, but they would be directly competing with scaup so that prey densities would need to be much higher to support both species.
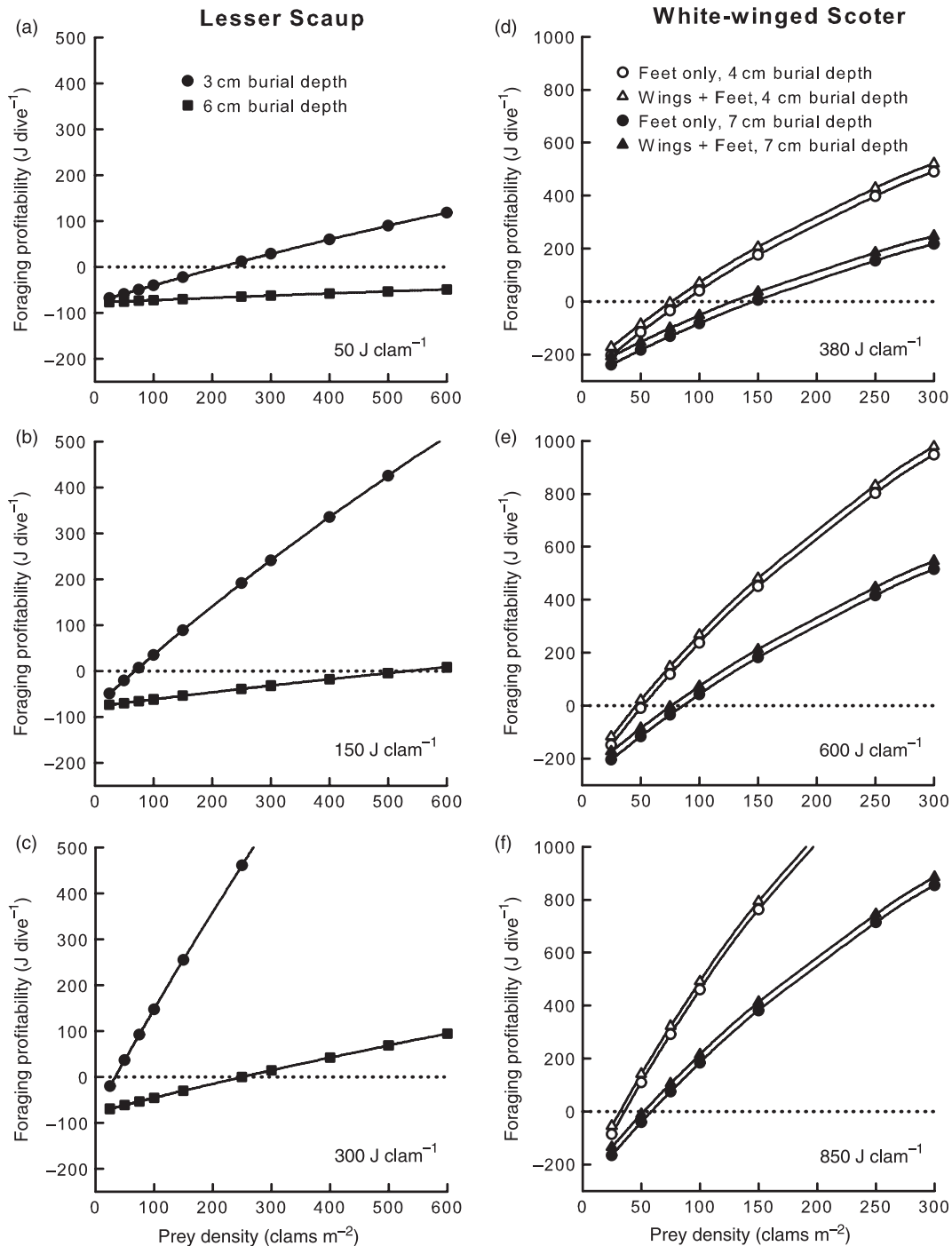
Fig. 1. Foraging profitability (FP, J dive^{-1}) for lesser scaup feeding on clams < 12 mm long with energy content of (a) 50, (b) 150 and (c) 300 J clam^{-1} buried at depths of 3 and 6 cm in the sediments, and for white-winged scoters feeding on clams 18–24 mm long with energy content of (d) 380, (e) 600 and (f) 850 J clam^{-1} buried at depths of 4 and 7 cm in the sediments. Assimilated energy intake rates (J dive^{-1}) for scaup and scoters at each prey density were generated from functional responses for the three energy values fit with nonlinear regression (Table 3). Foraging profitability curves were calculated by subtracting the cost of diving (J dive^{-1}) from the assimilated energy intake per dive for each prey density. Threshold food densities are where foraging profitability equals zero (Table 4).

Discussion

Our study has shown the importance of prey size and accessibility to threshold prey densities and the carrying capacity of a habitat for diving ducks of differing body size. While partitioning prey by size and depth can reduce competition between these different-sized predators, shifts in the size–depth structure of prey can greatly alter the relative ability of each predator to persist. Conversely, periodic disturbances that alter prey size–depth structure can create a mosaic of patches that favour predators of different body size; this effect could facilitate their coexistence on the same prey base
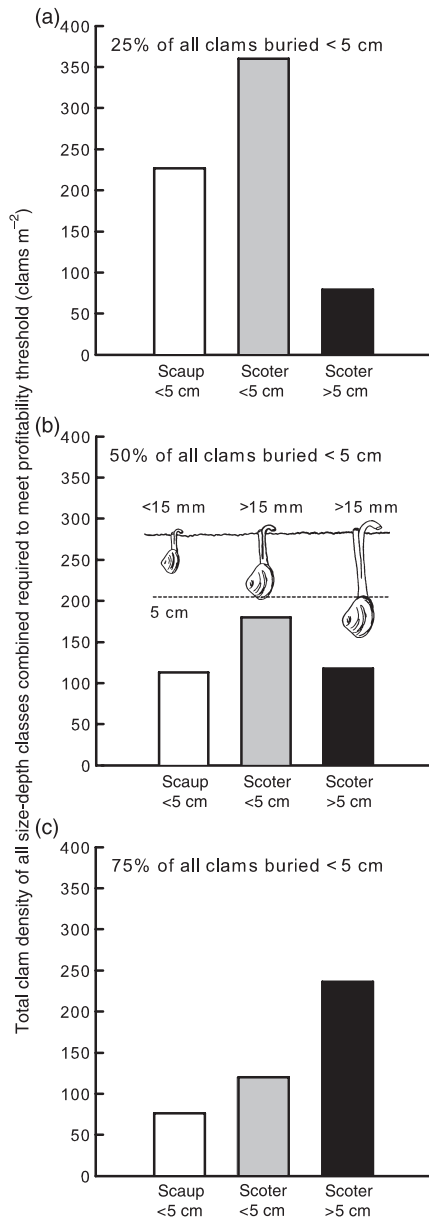
Fig. 2. Total clam densities (clams m^{-2}) of all size–depth classes combined that are needed to meet threshold energy requirements by scaup feeding on clams < 15 mm long at burial depths < 5 cm (white bars), and for scoters feeding on clams > 15 mm long at burial depths < 5 cm (grey bars) or > 5 cm (black bars) when (a) 25%, (b) 50% or (c) 75% of all clams were buried at depths < 5 cm (see Methods for details of size distributions).

in the same area. For diving ducks with similar foraging modes, whether the same total prey base will support fewer larger predators will vary with these factors.

CONSTRAINTS OF FORAGING MODE AND AVAILABLE TIME

Critical to models of profitability are estimates of the metabolic costs of foraging for species using different modes of locomotion underwater. While scaup use only foot propulsion underwater, scoters (like some other sea ducks such as

eiders *Somateria* spp. and long-tailed ducks *Clangula hyemalis*) can reduce costs of dives to shallow depths by > 34% by using their wings in addition to feet during descent (Richman & Lovvorn 2008). Drag-based propulsion (as by feet) is more effective for intermittent locomotion over short distances at slower speeds, whereas lift-based propulsion (as by hydrofoil wings) has much higher propulsive efficiency but requires greater travel distances and higher speeds (Vogel 2008). Thus, when scoters are manoeuvring in complex, shallow and densely vegetated habitats, using feet only is the better locomotor mode, whereas using both wings and feet is better when scoters are feeding in deeper, more open habitats. In the latter case, using wings + feet allows scoters to descend more rapidly, providing more time at the bottom for foraging (Richman & Lovvorn 2008).

Energy intake has to balance not only the cost of foraging itself, but also the energy costs of maintenance metabolism, thermoregulation and other activities throughout the diel period. Thus, depending on the amount of time available for foraging, intake rates at our calculated threshold densities will underestimate the intake rates needed for a bird to meet its daily energy requirements. While scaup are known to forage during both day and night (Nilsson 1970; Custer, Custer & Sparks 1996), scoters typically forage only during the day (Lewis, Esler & Boyd 2005). This limitation on foraging time may become increasingly important at higher latitudes when daylight hours are limited during winter (Goudie & Ankney 1986; Systad, Bustnes & Erikstad 2000).

SIZE- AND DEPTH-SPECIFIC PREDATION

Size-specific predation has been documented in diverse benthic predators, including birds (Zwarts & Wanink 1984; Lovvorn *et al.* 2003), fish (Arnott & Pihl 2000), crabs, lugworms and crangonid shrimp (Hiddink *et al.* 2002). Of the accessible fraction of prey, diving ducks often select clams of smaller length than expected (Draulans 1982, 1984; Bustnes & Erikstad 1990; de Leeuw & van Eerden 1992; Bustnes 1998; Hamilton, Nudds & Neate 1999). Although smaller-sized clams have lower energy content per prey item, numbers consumed per unit time are typically higher (Richman & Lovvorn 2003, 2004). Conversely, some prey are too large to be swallowed, too deep in the sediments or incur excessive handling costs (Reading & McGrorty 1978; Zwarts & Wanink 1984; Richman & Lovvorn 2003, 2004; Nolet *et al.* 2006). Avian predators can be constrained by their body size and bill morphology to an optimal range of prey sizes, depths in the sediments, dive depths and times spent foraging. The tufted duck (*Aythya fuligula*), a close congener to the scaup, was more size-selective as dive depth increased (Draulans 1982), presumably because higher costs or shorter bottom times made selection of optimal size more important.

Although larger body size incurs higher absolute energy requirements, larger scoters have a larger fraction of the total prey biomass accessible to them than is available to the smaller scaup. Through winter, as the fraction of preferred prey at shallow burial depths is depleted, scoters can forage profit-

ably on the remaining prey that are large and buried deeply at low densities (Fig. 2a). Because the smaller scaup are limited to small, shallow-burrowing prey, scaup will tend to be more limited by prey accessibility than the larger scoters. Conversely, our analyses suggest that a prey shift towards small, shallow-burrowing clams would allow scaup to persist at low total prey densities (>76 clams m^{-2}) while scoters would be forced to either eat smaller, lower energy prey items or search for other areas with larger prey (Fig. 2c).

CARRYING CAPACITY AND REQUIRED HABITAT AREA

Many studies have attempted to estimate the carrying capacity of a particular habitat area for different species, or conversely, to estimate the habitat area required to support given populations of those species. Some analyses have used allometric estimates of population density or area required for animals of a given body size (Silva & Downing 1994; Gaston & Blackburn 1996). Others have estimated (often allometrically) the energy required by the predator population, and then compared that value to either the total biomass of food, or the biomass above some level of maximum profitable depletion (Korschgen, George & Green 1988; Michot 1997; Goss-Custard *et al.* 2002; Durell *et al.* 2006; Miller & Eadie 2006). In this study, we have shown that for infaunal foods, the threshold of maximum depletion (giving up density) varies substantially with the size and associated depth distribution of prey. Thus, the same total prey density or biomass may or may not support profitable foraging by predators of different body sizes. Moreover, average prey sizes and burial depths may overlook the spatial heterogeneity in prey size structure that facilitates the coexistence of predators that partition the same prey taxa by size and burial depth. The net effect of this patch structure of size distributions will depend on the spatial scale and synchrony of disturbances that maintain the patch structure (Hall, Raffaelli & Thrush 1994).

Field sampling of infaunal clams in San Francisco Bay (Poulton *et al.* 2004), and of below-ground macrophyte tubers in a brackish inland lake (Lovvorn & Gillingham 1996), indicates that patchiness in food densities of diving ducks in these habitats is not predictable at scales of a few metres. Probably for this reason, shorebirds (Colwell & Landrum 1993; Cummings, Schneider & Wilkinson 1997) and rays (Hines *et al.* 1997) feeding in tidal sediments appear not to respond to patchiness at such small scales. However, small-scale variations, because they affect profitability, undoubtedly influence habitat selection at larger scales where average intake rates can be monitored by the predator (Vaitkus & Bubinas 2001).

Throughout North America and Europe, major wintering and migration areas for diving ducks have been degraded by industrial and urban development, altered sediment or nutrient loads, exotic species or hypoxic conditions (Seliger, Boggs & Biggley 1985; Cohen & Carlton 1998; Jaffe, Smith & Torresan 1998). For example, in San Francisco Bay, typical decrease in prey densities over the wintering period (Poulton *et al.* 2002, 2004), together with projected long-term declines

in the area of shallow soft-bottom habitats (Jaffe *et al.* 1998), has increased the need for estimates of carrying capacity and the extent of viable habitat for wintering scaup and scoters. We often assume that total prey density or biomass is a good measure of available foods. However, in conservation efforts for these and other species, we urge consideration of the size and accessibility of prey in its value to predators of different body sizes. These aspects can have major effects on the numbers of different predator species an area of habitat can support.

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