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Trophic Interactions Between Cormorants and Fisheries: Towards a More Quantitative Approach Using Stable Isotopes

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Abstract.—Double-crested Cormorants (*Phalacrcorax auritus*) and other piscivorous birds are frequently implicated in having negative effects on commercial and sport fisheries despite the fact that several studies suggest that such effects may be infrequent. Increases in cormorant populations in North America over the last decades have fueled the debate further and population controls, official and unofficial, are in effect in several jurisdictions. Of importance to the management community is the need to obtain the best information on actual diets of cormorants throughout their annual cycle but particularly on the temperate breeding grounds where they frequently overlap with fisheries. Despite success in quantifying seabird diets, managers have yet to exploit the potential of the stable isotope approach to examine trophodynamics of cormorants where they can potentially interfere with fisheries. Here, the use of stable isotope methods (δ^{15}N and δ^{13}C) to quantitatively predict trophic interactions between cormorants and their prey are recommended to augment conventional dietary approaches. The stable isotope approach is particularly suited to situations where birds feed at a single, well-defined lake or waterbody. The approach can provide a quantitative estimate of fish consumption to species or species groups in cases where such groups are isotopically distinct. This paper is intended to provide the research and management communities with the necessary background to apply stable isotope methods to better assess diets of cormorants and other piscivorous waterbirds. *Received 21 December 2007, accepted 28 June 2009.*

Key words.—Carbon-13, Double-crested Cormorants, nitrogen-15, *Phalacrocorax auritus*, stable isotopes, fisheries.

Recovery or increases in populations of Double-crested Cormorants (*Phalacrocorax auritus*) in North America have been met with concern over the potential impact this may have on sport and commercial fisheries, especially on their temperate freshwater breeding grounds (Nettleship and Duffy 1995; Wires and Cuthbert 2006). Indeed, concern over impacts to fisheries forms one of the key platforms of current and proposed management actions to reduce continental cormorant populations. Several previous studies have examined relative proportions of prey species in diets of cormorants and used this information to estimate the total biomass of commercially valuable species taken during the period the birds are present (e.g. Glahn and Brugger 1995; Johnston *et al.* 2002; Rudstam *et al.* 2004). Such information can assist with predictions of the role cormorants play as predators of various species and size classes of fish and can also allow a comparison of avian vs. human consumption for any given system.

As for many colonial waterbirds, cormorants are amenable to dietary analysis because nestlings and pre-fledged individuals readily regurgitate prey once disturbed on colonies and vast numbers of individual boluses of prey items can be obtained in a single visit to a colony (Hobson *et al.* 1989). Properly timed visits allow a reasonable assessment then of the diets of young birds and, if enough visits are conducted over the season, a reasonable picture of the relative importance of prey items to growing birds is possible. For adults, this approach is less effective because adults often flush before they are approached closely. Adult diet must then be inferred from the regurgitation of pellets

found at colonies or the direct examination of stomach contents through lethal collections or through stomach flushing if birds can be captured. Often stomachs are empty and typically provide a very short-term snapshot of individual diet. Adult diet is typically poorly known relative to the diet of young birds (Neuman *et al.* 1997; Forero *et al.* 2002; Hobson *et al.* 2002).

Understanding diets of waterbirds is fundamental to understanding their ecology and there has been much concern over the reliability of quantitative estimates based on conventional techniques such as stomach sampling, scat and pellet analyses or direct observation (Duffy and Jackson 1986). In the case of cormorants and other species that are of management concern, drawbacks of such conventional approaches are potentially serious. Fortunately, the development of stable isotope methods to quantitatively assess the relative contributions of isotopically distinct food types to the diets of consumers has provided an additional tool to assist investigators. However, despite the potential of this tool and the numerous applications of stable isotope measurements to infer diet or feeding location of seabirds including cormorants (Mizutani *et al.* 1990, 1991; Hobson *et al.* 1994; Bearhop *et al.* 1999; Forero and Hobson 2003), the approach has hitherto not been embraced by researchers and managers interested in the impacts of Double-crested Cormorants and other species on commercial and sport fisheries. The purpose of this paper is to provide the necessary background required to understand and apply the stable isotope method to investigating interactions between cormorants or other piscivorous waterbirds and their fish prey base.

Stable Isotopes in Ecological Studies

There are several texts that are useful in applying stable isotopes in ecological studies (Kelly 2000; Martinez del Rio and Wolf 2005; Karasov and Martinez del Rio 2007; Michener and Lajtha 2007; Inger and Bearhop 2008). Here, emphasis will be placed on the elements carbon and nitrogen both of which have two stable isotopes (^{13}C, ^{12}C; ^{15}N, ^{14}N)

but additional information is possible from the measurement of the isotopes of sulfur (^{34}S, ^{32}S), hydrogen (^{2}H, ^{1}H) and oxygen (^{18}O, ^{16}O). In all applications of stable isotope methods in ecological studies, we are interested in the relative abundance of the heavier to lighter isotope (e.g. ^{13}C/^{12}C; ^{15}N/^{14}N) expressed in delta (δ) notation relative to international standards (e.g. δ^{13}C, δ^{15}N).

Isotopic Discrimination and Foodwebs

Carbon and nitrogen enter foodwebs with stable isotope ratios that reflect a number of possible biogeochemical processes. In aquatic foodwebs, a prime determinant of these ratios is the corresponding ratios in inorganic nutrients (Finlay and Kendall 2007). Plant photosynthetic pathway can further dramatically alter the isotopic ratio of fixed carbon and this resembles a C3 pathway for most freshwater aquatic systems. Dissolved inorganic nitrogen (DIN) isotope values will influence foodweb δ^{15}N values. Once fixed at the base of the foodweb in primary production, stable isotope values in consumer and prey typically undergo a step-wise enrichment with trophic level:

$$\delta X_t = \delta X_d + \Delta_{dt} \qquad (1)$$

where δX_t is the stable isotope ratio of the tissue (t) in the consumer, δX_d the stable isotope ratio of the diet (d) and Δ_{dt} is the isotopic discrimination factor between diet and consumer tissue. So, if we know Δ_{dt} and δX_t, we can derive δX_d through subtraction. Put another way, we can predict the stable isotope value of the prey if we measure the stable isotope ratio in a given consumer's tissue for which we know the appropriate discrimination factor associated with that tissue.

Determination of the appropriate isotopic discrimination factor for the consumer of interest provides an extremely powerful means to infer the isotopic value of the diet. Moreover, if we know the discrimination factors associated with each trophic step from primary production, it is possible to reconstruct the trophic position of the consumer of interest. Trophic position is a much more

useful currency than the stable isotope value alone. Even though we know that the magnitude of the isotopic discrimination factor can change across trophic steps, most researchers have previously assumed a constant enrichment factor can be applied within foodwebs and have used this to model trophic position.

Table 1 summarizes our state of knowledge for isotopic discrimination factors between diet and whole blood or feathers of waterbirds. These studies range from those opportunistic investigations using captive zoo animals with varying assumptions concerning the isotopic homogeneity of diets (Mizutani *et al.* 1992) to careful experimental studies designed to control diets as carefully as possible (Evans-Ogden *et al.* 2004). While there is considerable variation in derived diet-tissue discrimination factors, the overall means of +0.7 and +2.7‰ for blood, and +1.5 and 4.0‰ for feather $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ values, respectively, provides a useful first approximation for diet and trophic modeling if birds can be captured (Fig. 1; see also Post 2002). In cases where birds are taken lethally, stable isotope measurements of muscle and liver tissues can also provide estimates of diet but the diet-tissue isotope value for these tissues is less well known (Table 1).

Aquatic foodwebs have isotopic structure that roughly corresponds to strong trophic effects on $\delta^{15}N$ values, weaker trophic effects on $\delta^{13}C$ values, and strong effects on $\delta^{13}C$ of algal or benthic vs. phytoplankton or pelagic sources of primary production. Using a dual isotope approach can readily assist us in identifying dietary dependence on fish groups that differ trophically (i.e. primarily using $\delta^{15}N$ values; Hobson *et al.* 1994) as well as in their relative dependence on zooplankton and zoobenthos (i.e. using $\delta^{13}C$ values; Hobson and Welch 1992; France 1995; Vander Zanden and Vadeboncoeur 2002).

Dietary Integration and the Isotopic Clock

Previous researchers have estimated the isotopic turnover rates for various animal tissues using captive studies. The uptake of the new isotopic dietary signal is traced until

equilibrium conditions are reached and an exponential equation of the form:

$$\delta X(t) = a + be^{(-\lambda t)} \qquad (2)$$

where $\delta X(t)$ is the stable isotope value of a given tissue as a function of time, *a* is the asymptotic tissue value, *b* is the magnitude of the isotopic shift in diets, and λ is the fractional rate of isotope incorporation. Curves of this form fit the empirical data well but recent advances have been made that linearize the relationship to account for more than one potential isotopic pool contributing to the tissue isotope turnover (Cerling *et al.* 2007; but see Wolf *et al.* 2009). Based on the avian survey of Carleton and Martínez del Rio (2005), we expect the turnover of carbon in whole blood to approximately follow the relationship:

$$\text{half life}(m) = 7.6\log(m) - 1.2 \qquad (3)$$

So, for a cormorant with a body mass of 2300g, the approximate half life of carbon in whole blood is 24.4 d. This suggests that blood measurements in cormorants reflects at least two months of dietary integration (i.e. > two half lives). For chicks, obviously the period of integration will be less, depending on the age of the individual and a component of turnover related to growth can also be modeled (Wolf *et al.* 2009).

A useful aspect of isotopic applications is that different tissues from the same individual will provide information on diet for different time periods. If carcasses are available, the analysis of liver stable isotope values will provide relatively short periods of dietary integration (of the order of a week for a cormorant) whereas muscle or whole blood, will provide information on diet over a period of about a six weeks. Bone collagen, with extremely slow turnover, can represent the lifetime average diet of an adult but will be biased to the period of bone growth in younger birds. If non destructive sampling is possible, then blood plasma and cellular fractions provide the same periods of integration as liver and muscle, respectively. Feathers will also provide dietary information for the period of

Table 1. Summary of isotopic discrimination between diet and tissues for waterbirds. Only those studies that removed lipids from dietary samples in calculations of $\delta^{13}C$ discrimination factors were used. The asterisk corresponds to cases where whole (lipid-free) dietary items were used. All other cases correspond to cases where dietary (lipid-free) muscle tissue was used.

Species	N	Discrimination factors (‰)		Source
		$\delta^{13}C$	$\delta^{15}N$	
WHOLE BLOOD				
King Penguin (*Aptenodytes patagonica*)	9	-0.8	2.1	Cherel *et al.* (2005)*
	9	-0.6	1.2	Cherel *et al.* (2005)
Rockhopper Penguin (*Eudyptes chrysocome*)	11	0.0	2.7	Cherel *et al.* (2005)*
	11	0.5	1.9	Cherel *et al.* (2005)
Ring-billed Gull (*Larus delawarensis*)	14	-0.3	3.1	Hobson and Clark (1992)
Great Skua (*Catharacta skua*)	9	1.1	2.8	Bearhop *et al.* (2002)
	9	2.3	4.2	Bearhop *et al.* (2002)
Dunlin (*Calidris alpina pacifica*)	4	1.3	2.9	Evans Ogden *et al.* (2004)
Tufted Puffin (*Fratercula cirrhata*)		-0.3	3.1	Williams et al.(2007)
Mean		0.4	2.7	all
		0.6	2.7	Excluding (*)
FEATHERS				
Humboldt's Penguin (*Spheniscus humboldti*)	16	—	4.8 ± 0.5	Mizutani *et al.* (1992)
King Penguin (*Aptenodytes patagonica*)	9	0.3	2.7	Cherel *et al.* (2005)
	9	0.1	3.5	Cherel *et al.* (2005)*
Rockhopper Penguin (*Eudyptes chrysocome*)	11	0.1	4.4	Cherel *et al.* (2005)*
	11	0.6	3.5	Cherel *et al.* (2005)
Common Cormorant (*Phalacrocorax carbo*)	17	—	3.7	Mizutani *et al.* (1992)
	8	2.3	4.2	Bearhop *et al.* (1999)
European Shag (*Phalacrocorax aristotelis*)	12	2.0	3.6	Bearhop *et al.* (1999)
Ring-billed Gull (*Larus delawarensis*)	14	0.2 ± 1.3	3.0 ± 0.2	Hobson and Clark (1992)
Black-tailed Gull (*Larus crassirostris*)	22	—	5.3 ± 0.8	Mizutani *et al.* (1992)
Great Skua (*Catharacta skua*)	24	2.1	4.6	Bearhop *et al.*, 2002
Common Murre (*Uria aalge*)	11	2.5 ± 0.2	3.6 ± 0.2	Becker *et al.* (2007)
	11	1.9 ± 0.3	3.7 ± 0.2	Becker *et al.* (2007)
	8	1.0 ± 0.1	3.3 ± 0.4	Thompson and Furness (1995)
Arctic Tern (*Sterna paradisaea*)	8	2.1 ± 0.1	3.4 ± 0.2	Thompson and Furness (1995)
Nankeen Night Heron (*Nycticorax caledonicus*)	8	—	4.2 ± 0.3	Mizutani *et al.* (1992)

Table 1. (Continued) Summary of isotopic discrimination between diet and tissues for waterbirds. Only those studies that removed lipids from dietary samples in calculations of $\delta^{13}C$ discrimination factors were used. The asterisk corresponds to cases where whole (lipid-free) dietary items were used. All other cases correspond to cases where dietary (lipid-free) muscle tissue was used.

| Species	N	Discrimination factors (‰)			Source
		$\delta^{13}C$	$\delta^{15}N$		
Great White Egret (*Egretta alba*)	4	—	3.9 ± 0.2		Mizutani *et al.* (1992)
Grey Heron (*Ardea cinerea*)	8	—	4.3 ± 0.4		Mizutani *et al.* (1992)
Scarlet Ibis (*Eudocimus ruber*)	18	—	4.5 ± 0.4		Mizutani *et al.* (1992)
White Ibis (*Eudocimus albus*)	23	—	4.3 ± 0.5		Mizutani *et al.* (1992)
Flamingo (*Phoenicopterus* spp.)	14	—	5.6 ± 0.3		Mizutani *et al.* (1992)
Mean		1.3	4.0	all	
		1.5	4.0	Excluding (*)	
MUSCLE					
Ring-billed Gull (*Larus delawarensis*)		0.3	1.4		Hobson and Clark (1992)
Great Cormorant (*Phalacrocorax carbo*)		1.3	2.4		Mizutani *et al.* (1992)
LIVER					
Ring-billed Gull (*Larus delawarensis*)		-0.4	2.7		Hobson and Clark (1992)
Great Cormorant (*Phalacrocorax carbo*)		4.2	4.8		Mizutani *et al.* (1992)
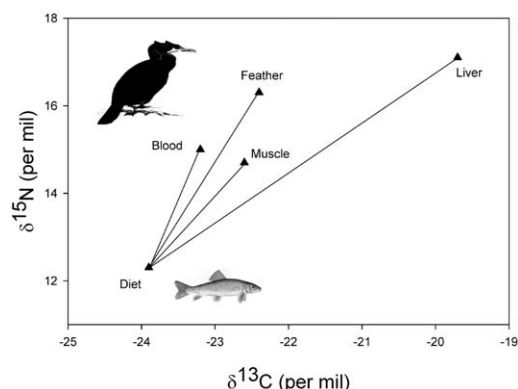
Figure 1. Depiction of isotopic discrimination between diet and blood, feathers, muscle and liver expected for cormorants and other piscivorous waterbirds. Here, discrimination factors from Mizutani _et al._ (1992) were used for muscle and liver and mean values from Table 1 for blood and feathers.
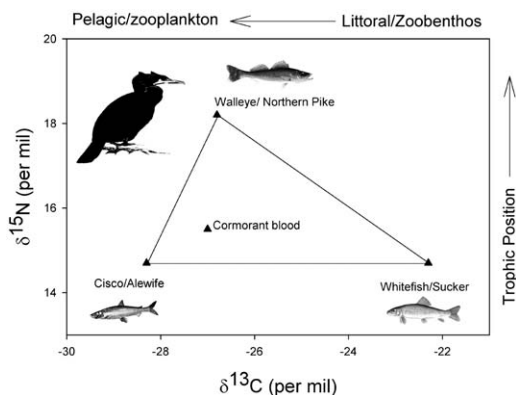

Figure 2. Hypothetical mixing model for cormorant blood with three possible isotopically distinct dietary endpoints. Note that each endpoint represents the value of cormorant blood expected from an exclusive diet of that prey group. Model based on average discrimination factors for blood shown in Table 1.

growth and so are an excellent means of delineating diet for the post-breeding period. Claws are continuously growing and so provide the opportunity to sample over relatively long periods of integration (due to slow growth). So, a recently arrived bird on the breeding grounds is expected to have claws corresponding to the winter growth period.

Mixing Models

When isotopically distinct dietary items are available to a consumer, the relative inputs of these items can often be calculated using mixing models. The general rule-of-thumb is that it is possible to delineate the contributions of n isotopically distinct inputs using n - 1 stable isotopes (Phillips and Gregg 2001). So, for studies using $\delta^{15}N$ and $\delta^{13}C$ measurements of cormorant tissues, it is possible to infer dietary inputs from three isotopically distinct prey types. The so-called isotopic endpoints representing three groups of fish are depicted in Fig. 2 loosely based on real isotopic data of fish communities summarized in Vander Zanden and Vadeboncoeur (2002). Endpoints shown in Fig. 2 represent the values one would expect for cormorant tissues if they fed 100% on that endpoint and so are derived from actual fish muscle tissue corrected for isotopic discrimination to cormorant blood. Similar

models could be used for any cormorant tissue providing the diet-tissue isotope discrimination factors are known for that tissue type. Fortunately, software is freely available from the U.S. Environmental Protection Agency (EPA) that allows the quick calculation of relative inputs based on n inputs and n-1 stable isotopes (http://www.epa.gov/wed/pages/models/stableIsotopes/isotopes.htm, accessed June 26 2009). Also, recent advancements have now been made that use a Bayesian statistical treatment for isotopic mixing models (see http://statacumen.com/sisus/, accessed June 26 2009). The hypothetical example shown in Fig. 2 assumed a cormorant blood isotope value of 15.5‰ ($\delta^{15}N$) and has the solution of 61.2% cisco/alewife, 16.0% whitefish/sucker and 22.9% walleye.

A useful refinement of the mixing model approach has been the use of probabilistic models for coping with situations where there are more than n isotopically distinct inputs to diets when using n - 1 isotopes (Phillips and Gregg 2003). This provides a means of delineating ranges of possible solutions that place maximum and minimum limits on the possible input of any particular prey or prey species group (e.g. Urton and Hobson 2005). Readers should be aware that mixing models are based on several assumptions including dietary equilibria, lack of metabolic routing, and equal digestibility of various prey types.

Also, while not presented here, there is also a need to associate error estimates to derived prey contributions. Software developed by the EPA is available for this purpose.

Isotopic Template for Estimating Cormorant Diet

The Common Currency of Trophic Level. A major benefit of using stable isotopes to quantify diet of Double-crested Cormorants or other piscivorous waterbirds is that they often forage in a single lake or waterbody. This provides the opportunity to establish the isotopic structure of the aquatic foodweb leading to birds. In addition, since different waterbodies may have different baseline isotopic signatures of primary production, isotopic values of consumers in one system are not always identical to those of the same consumers in another system even if their feeding ecology and trophic position remain the same. One way of rendering isotopic data comparable among systems is to convert isotope data to trophic level (TL) based on $\delta^{15}N$ measurements, or to normalize foodweb $\delta^{15}N$ values to that of a primary herbivore such as a filter feeding bivalve (Vander Zanden *et al.* 1997). Ideally, TL of cormorants would be derived after establishing isotopically the TL of all foodweb components. Trophic level determinations using stable isotope values entail measurements of primary production (TL1), primary herbivores (TL2), primary carnivores (TL3), secondary carnivores (TL4) and so on. Such an approach will be particularly appropriate in systems that are well studied isotopically due to interest in sources of primary production, fish and invertebrate ecology, contaminant flow, and foodweb energetics in general (Hobson and Welch 1992; Cabana and Rasmussen 2002; Vander Zanden and Rasmussen 2001). Here, cormorant investigations could be a simple addition to an established isotope model using the diet-tissue isotopic discrimination factors derived from Table 1. In cases where isotopic (aquatic) foodweb models do not exist, useful management information could be based on the delineation of cormorant TL following the measurement of the basic trophic guilds of fish available to cormorants. An evaluation of cormorant TL relative to that of forage fish vs. piscivorous fish is a useful approach that can be used in the absence of detailed foodweb isotope data. In the example depicted in Fig. 2, a cisco/alewife forage fish TL of the order of 3.0-3.5 and a walleye/pike TL of the order of 4.0-4.5 is used. In the hypothetical system depicted in Fig. 2 with forage fish arbitrarily set at TL 3, the TL of cormorants would be as follows:

$$TL_{corm} = 3 + (\delta^{15}N_c - \delta^{15}N_f)/2.7 \qquad (4)$$

Where $\delta^{15}N_c$ is the $\delta^{15}N$ value of the cormorant tissue, $\delta^{15}N_f$ that of the forage fish and 2.7‰ is the diet-tissue discrimination factor between diet and cormorant blood.

The Common Currency of Percent Littoral Input. Quantifying the relative use of prey dependent on zooplankton vs. zoobenthos using $\delta^{13}C$ measurements is possible. Here, we rely on the isotopic enrichment of phytoplankton vs. macrophyte or algal forms of primary production. Vander Zanden and Vadeboncoeur (2002) provide an approach for standardizing lake fish samples to the percent reliance on zooplankton vs. zoobenthos secondary production:

% Contribution of Littoral =
$$(\delta^{13}C_f - \delta^{13}C_p)/(\delta^{13}C_l - \delta^{13}C_p) \qquad (5)$$

Where $\delta^{13}C_f$, $\delta^{13}C_l$, and $\delta^{13}C_p$ are the mean $\delta^{13}C$ of the (fish) consumer, littoral prey, and pelagic prey, respectively. Equation 5 assumes no isotopic discrimination for $\delta^{13}C$ at each trophic level but could readily be modified to assume a 1‰ value (or whatever). To make this useful for an analysis of percent take of cormorants of littoral secondary production, the following equation, using Equation 1, could be used:

% Contribution of Littoral =
$$([\delta^{13}C_c - \Delta_{dt}] - \delta^{13}C_p)/(\delta^{13}C_l - \delta^{13}C_p) \qquad (6)$$

Where Δ_{dt} is the appropriate $\delta^{13}C$ diet-tissue isotopic discrimination factor (i.e. +0.7‰ for blood and +1.4‰ for feather).

To summarize, if cormorant isotope data are to be compared among different popula-

tions, it is necessary to convert those isotope values to a common currency of TL and percent littoral input to diets because different aquatic foodwebs can be labeled differently at the level of primary production. In cases where only a single population is considered that feeds on a single aquatic foodweb, then a mixing model approach will likely be the most useful.

Other Considerations

The stable isotope approach will augment and not replace conventional dietary techniques previously used to assess the diets of cormorants and other piscivorous waterbirds. Stable isotope measurements are good estimators of trophic position and dependence on littoral vs. pelagic foodwebs. However, stable isotope models are often poor at providing detailed taxonomic information and so cannot typically distinguish species of prey within trophic or ecological guilds. The careful combination of conventional and isotopic approaches, together with other tools like fatty acid analyses, will provide the most complete picture. Whereas the isotope technique will provide the best estimates of total biomass being taken by trophic level and benthic vs. pelagic guilds, conventional dietary analyses will be extremely useful for estimating percent biomass allocations within these categories, especially for chicks whose diets can be estimated reasonably well with colony visits. However, stable isotope models can provide some key advantages. First, they provide information on assimilated and not just ingested foods. Second, they can provide an unbiased estimate of these diet types because they are not hampered by the shortcomings of biases associated with conventional approaches. Third, they provide time-integrated information that represents days to months of dietary integration depending on the tissue chosen.

While the determination of trophic level *per se* may seem a crude instrument with which to inform management decisions, the clear delineation between predatory game fish and forage fish appears to be a main point of contention with the management of cormorants in North America. Of course,

low trophic-level feeding does not necessarily mean birds are not taking younger life stages of commercially important species as most such species increase trophic position with length and age (Hobson and Welch 1995; McCarthy *et al.* 2004). Additionally, comparing trophic levels of cormorants with high trophic-level game fish can presumably inform questions of competition between these two predators. However, overwhelmingly, cormorants take smaller (median 12 cm) fish in proportion to their abundance (Durham 1955; Glahn *et al.* 1998; Hobson *et al.* 1989; Campo *et al.* 1993) and so managers will need to consider the likely or possible proportion of commercially valuable fish within the overall population of (low trophic level) small fish available to birds. Such considerations should also consider, of course, the possible positive effects of removal of small size classes on the average size of commercially valuable fish.

Finally, many freshwater and marine systems used by cormorants contain an impressive variety of prey species of varying ecology and isotopic signature. Indeed, some of these systems are so complex isotopically, or contain so many species at a given trophic level, that a simple two-isotope, three-source or multisource model will not provide particularly useful information. While it is possible that the addition of other isotopic measurements including $\delta^{34}S$ and, more recently δ^2H and $\delta^{18}O$ (Hobson and Wassenaar, unpub. data), will assist in delineating useful dietary information, there will be cases where the isotope approach will simply be of little use. This would also be the case if birds foraged at a number of different water bodies that differ isotopically.

Given the seriousness of current and proposed management actions aimed at reducing cormorant populations in order to benefit commercial and sport fisheries, it behooves us to better understand cormorant diets across their range. This would better provide the first step in understanding if cormorants negatively impact fisheries. Establishing a more accurate understanding of cormorant trophic level will allow better estimates of fish biomass taken using energetics

models. Currently, blood and prey samples taken from juvenile cormorants during colony visits can provide key information for dietary estimates based on several weeks of assimilation. In those cases where adults are being killed for control measures there is simply no excuse not to archive tissue samples from a sample of these birds to be used in future isotopic analyses. The cost of isotope analyses for carbon and nitrogen is relatively low (of the order of $10-15 US per sample) compared to the costs of control measures.

Designing Studies

Ideally, the use of stable isotope methods to assess diets of cormorants and their potential impact on fisheries would take in to account all sources of error and isotopic variance in both birds and their potential prey. It is typically impossible to predict the magnitude of isotopic variance in foodweb components *a priori* and so pilot assays are encouraged. The primary objective will be to describe the isotopic range of prey types encountered and to ensure that all prey trophic levels are adequately covered so that an isotopic biplot of (typically) $\delta^{15}N$ and $\delta^{13}C$ values will incorporate both trophic and benthic vs. pelagic components. Any prior knowledge of bird diet will of course be invaluable here and can inform Bayesian based mixing models. Sample sizes of prey for each category (including various size classes within species) will be at least 5-7 individuals and care will be taken to sample over a broad spatial context as large waterbodies can be structured isotopically due to various inputs of inorganic and organic nutrients (Wassenaar and Hobson, unpub. data).

The optimal time period of sampling of prey will depend on the tissue used. The use of feathers will require an understanding of the foodweb isotopic pattern late in the season whereas sampling muscle or blood will correspond more to 3-4 weeks within the sampling period. Seasonal changes in stable isotope values of prey are possible and generally poorly understood for most systems and so matching foodweb sampling with bird tissue dietary integration periods will be appropriate. Lipids will be removed from prey and bird muscle samples allowing a protein pathway to be modeled. Where possible, non-destructive sampling of birds is encouraged, something easily achieved on colonies with nestlings but more difficult with adults.

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