GREAT CORMORANT *PHALACROCORAX CARBO SINENSIS*
DIET AND ITS EFFECT ON FISH POPULATIONS AND THEIR
COMMUNITY IN THE EUTROPHIC CURONIAN LAGOON
ECOSYSTEM

Summary of doctoral dissertation

Biomedical sciences, ecology and environmental science (03 B)

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Scientific Supervisor:
Dr. Linas Ložys (Institute of Ecology of Nature Research Centre, biomedical sciences, ecology and environmental science – 03 B)

Consultant Supervisor:
Dr. Harry K. Gorfine (Melbourne University (Australia), biomedical sciences, biology – 01 B)

The defense of the doctoral dissertation is held at Vilnius University Ecology and Environmental Research Council:

Chairman:
Doc. dr. Zita Gasiūnaitė (Coastal Research and Planning Institute, Klaipėda University, biomedical sciences, ecology and environmental science – 03 B)

Members:
Habil. dr. Mečislovas Žalakevičius (Institute of Ecology of Nature Research Centre, biomedical sciences, ecology and environmental science – 03 B)
Prof. habil. dr. Algimantas Paulauskas (Vytautas Magnus University, biomedical sciences, biology – 01 B)
Prof. dr. Artūras Razinkovas-Baziukas (Coastal Research and Planning Institute, Klaipėda University, biomedical sciences, ecology and environmental science – 03 B)
Dr. Jūratė Lesutienė (Coastal Research and Planning Institute, Klaipėda University, biomedical sciences, ecology and environmental science – 03 B)

Opponents:
Dr. Tomas Virbickas (Institute of Ecology of Nature Research Centre, biomedical sciences, ecology and environmental science – 03 B)
Dr. Tomas Didrikas (AquaBiota Water Research (Sweden), subsidiary of Norwegian Institute for Water Research (NIVA), biomedical sciences, biology – 01 B)

Defense of dissertation will be held at the public session of the Vilnius University Ecology and Environmental Research Council on 23 November 2012 at 2p.m at the Institute of Ecology of Nature Research Centre.
Address: Akademijos st. 2, LT-08412, Vilnius, Lithuania
Tel.: +370 5 2729257, fax.: +370 5 2729352.

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DIDŽIOJO KORMORANO *PHALACROCORA X CARBO SINENSIS* MITYBA IR POVEIKIS ŽUVŲ POPULIACIJOMS BEI JŲ BENDRIJAI KURŠIŲ MARIŲ EUTROFINĖJE EKOSISTEMOJE

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Biomedicinos mokslai, ekologija ir aplinkotyra (03 B)

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Mokslinis vadovas:
Dr. Linas Ložys (Gamtos tyrimų centro Ekologijos institutas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)

Konsultantas:
Dr. Harry K. Gorfine (Melburno Universitetas (Australija), biomedicinos mokslai, biologija – 01 B)

Disertacija ginama Vilniaus Universiteto ekologijos ir aplinkotyros mokslo krypties taryboje:

Pirmininkas:
Doc. dr. Zita Gasiūnaitė (Baltijos pajūrio aplinkos tyrimų ir planavimo institutas, Klaipėdos universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)

Nariai:
Habil. dr. Mečislovas Žalakevičius (Gamtos tyrimų centro Ekologijos institutas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)
Prof. habil. dr. Algimantas Paulauskas (Vytauto Didžiojo universitetas, biomedicinos mokslai, biologija – 01 B)
Prof. dr. Artūras Razinkovas-Baziukas (Baltijos pajūrio aplinkos tyrimų ir planavimo institutas, Klaipėdos universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)
dr. Jūratė Lesutienė (Baltijos pajūrio aplinkos tyrimų ir planavimo institutas, Klaipėdos universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)

Oponentai:
Dr. Tomas Virbickas (Gamtos tyrimų centro Ekologijos institutas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B)
Dr. Tomas Didrikas (Norvegijos vandens tyrimų institutas, mokslinių tyrimų padalinys AquaBiota (Švedija), biomedicinos mokslai, biologija – 01 B)

Adresas: Akademijos g. 2, LT-08412, Vilnius, Lietuva
Tel.: +370 5 2729257, faks.: +370 5 2729352.

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Introduction

Relevance of the study. The rapid expansion of Great Cormorant *Phalacrocorax carbo sinensis* populations in Europe during the second part of the 20th century has caused many conflicts, mostly with fishing and aquaculture. Fishermen often consider cormorants as one of the most important reasons for depleted fish stocks. There is much documentary evidence showing cormorant damage in aquaculture ponds, as well as negative impact in small or low productivity water bodies (e.g. Davies et al. 2003, Stewart et al. 2005). However, evaluations of cormorant impact on fish populations and commercial landings in larger water bodies are often ambiguous, particularly such as the shallow, highly productive waters of Curonian Lagoon, although fish consumption might be substantial (Mous 2000, Engström 2001). Most of these studies have not shown that significant changes of fish communities are related to increases in cormorant numbers (e.g. Eschbaum et al. 2003, Stempniewicz et al. 2003a, Žydelis and Kontautas 2008).

The biology of the Great Cormorant is well known, as it is the most studied wild bird in Europe; it’s diet is also known as well as approximate biases in diet study methods. The International Council for the Exploration of the Sea (ICES) reviewed the scientific literature about the impact of cormorants on fisheries in Europe and identified issues which are important for the further study, quantification and understanding of cormorant-fishery interactions. ICES noted that the overall impact of predation by cormorants on their prey populations and the consequences for fish community interactions are not well known. There have been very few studies by fish population biologists. ICES highlighted the need for population studies of relevant prey species of cormorants, including research on fish population dynamics, particularly the role of cormorants compared to other factors (ICES 2009). Fish population data based on long-term time series are often lacking for the assessment of cormorant impact and accurate measurement of consumption is often complex. Aspects of cormorant diet research necessary for evaluating the impact on fish populations include estimation of qualitative and quantitative dietary composition, long-term and seasonal changes, species and size selectivity, and prey fish consumption. Ichthyological research is also needed to assess fish community composition and dynamics, and to estimate fish population parameters.

Aim of the study is to assess Great Cormorant, breeding at the Juodkrantė colony, diet and their impact on fish populations and their community in the Curonian Lagoon.

Study objectives:
1. to assess Great Cormorant qualitative and quantitative diet composition at the Juodkrantė colony, including its variation over time, feeding selectivity and identifying main prey fish species;
2. to evaluate the reliability of pellet analysis method for quantitative diet assessment using a stable isotope mixing model;
3. to assess the importance of water bodies for Great Cormorant feeding and fish consumption;
4. to estimate the importance of commercial fish species in the diet and competition between fisheries and Great Cormorants;
5. to evaluate Great Cormorants impact on fish populations and their community in the Curonian Lagoon using spatial ichthyological survey and long-term fish monitoring data.
**Scientific novelty of the study.** This study is the first evaluation of Great Cormorant impacts on their main prey fish populations in the southern Baltic region, where one of the largest cormorant expansions has occurred during the last two decades. Data from long-term monitoring of Curonian Lagoon fish populations and comprehensive sampling of Great Cormorant diets were used for the impact evaluation. Great Cormorant impact on spatial fish distribution was also assessed for the first time. These results make substantial contributions towards evaluating cormorant impacts, and understanding the mechanisms of Great Cormorant colony regulation. The reliability of traditional analytical methods for quantitative dietary assessments was evaluated for the first time by comparing the results from pellet analysis with those calculated using a stable isotope mixing model.

**Scientific and practical significance.** The results of our study are important for providing improved assessments of the long-term effects of Great Cormorants on fish communities in large, complex, highly productive aquatic systems. This study is one of very few that have been undertaken using long-term cormorant diet and fish community data. Aspects of cormorant nutrition, important for evaluating the impact on fish populations, were determined. These included temporal variation in diet composition and reliability of methods for quantifying the composition of diets. Importantly, the results presented identify key aspects for further research into the impact of cormorants on fish populations. Cormorant diet selectivity parameters allow estimation of responses of the major prey fish species cohorts to selective foraging by cormorants.

The practical significance of this study is its evaluation of direct and indirect competition between cormorants and commercial fishermen. Although the amount of biomass consumed may not necessarily influence commercial landings, evaluation of the extent of competition enables the need for measures to regulate cormorant populations to be substantiated. In addition to assessing the impact of cormorants on native species, future assessments of their impact on invasive Round Goby populations might also become important.

**Defensive statements.**
1. Pellet analysis is sufficiently precise as a method for quantifying cormorant diet composition;
2. Composition of diets among Great Cormorants at the Juodkrantė colony differs among years and spring-summer seasons;
3. The Curonian Lagoon is the main feeding ground of Great Cormorants at the Juodkrantė colony;
4. Great Cormorant fish consumption in the Juodkrantė colony is both species and size selective;
5. Great Cormorant impacts are not large enough to cause noticeable changes of fish abundance within the vicinity of the Juodkrantė colony;
6. Neither total, nor the most important prey fish species biomass of the Curonian Lagoon did not change significantly during the time interval, covering periods of low Great Cormorant abundance, through an exponential increase in numbers, to a stable period of high abundance.
7. Increases observed in the size of the Great Cormorant population neither caused changes in the abundance of the most important prey fish species, nor in the total fish biomass of the Curonian Lagoon;

8. Great Cormorants are effectively adapting to changes in food resources by changing their foraging strategy. The invasive Round Goby, which is spreading in the Curonian Lagoon and the Baltic Sea, has become one of the main fish species in the cormorant diet within a short period of time.

**Scientific approval.** Four publications were published on the dissertation topic. Results of the study were presented at 7 international conferences.

**Structure and volume of the dissertation.** The dissertation consists of the following chapters: Introduction, Literature review, Study area, Material and methods, Results, Discussion, Conclusions and References. The dissertation comprises 151 pages. Observations and results are presented in 37 figures and 11 tables. The list of author’s publications comprises four peer reviewed scientific papers. The reference list contains 302 sources. The dissertation is written in Lithuanian with an English summary.

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**Literature review**

The chapter, comprising six parts, deals with the taxonomy, main biological features, and spatial distribution of Great Cormorants. Different aspects of cormorant foraging biology and diet study methods are extensively reviewed. Causes of Great Cormorant population expansion and the consequent conflicts and their patterns across Europe are also discussed. In-depth consideration is given to research about cormorant impacts on fish populations and investigations of Great Cormorants in Lithuania.

**Study area**

This study of the Great Cormorant diet took place in the largest Lithuanian colony located on the Curonian Spit near the Juodkrantė settlement (Fig. 1). The number of breeding pairs in the colony varied around 3,000 (from 2,362 to 3,367) during the study period in 2005–2010. The colony is about 200 m distance from the Curonian Lagoon and 800 m from the Baltic Sea. Great Cormorant impacts on fish populations were investigated in the Lagoon. The Lagoon is a highly productive, shallow, eutrophied freshwater body that is intensively exploited by the commercial fishery. Considering that Great Cormorants forage up to 35 km from the colony (Gremillet et al. 1999a, Paillisson et al. 2004), their feeding area approximately covers the entire Lithuanian part of the Lagoon. Great Cormorants forage up to depth of 20 m (Van Eerden et al. 1995), and such depths in the Baltic Sea shore zone are about 2–3 km offshore from the Curonian spit. Eighty-two fish and lamprey species are registered in the Curonian Lagoon and the Lithuanian economic zone of the Baltic Sea (Repečka 2003a, Bacevičius and Karalius 2008, Ložys 2008, Bacevičius 2009, Bagdonas et al. 2011). Nineteen species are commercially targeted in the Sea and twenty-seven in the Lagoon.

**Material and methods**

Great Cormorant diet composition was studied using the conventional pellet analysis method (Carss et al. 1997). The study was implemented in 2005–2010 at the Juodkrantė cormorant colony. Pellets were sampled during the breeding season from the end of March until the birds left the colony at the beginning of August. In total 1032 pellets were analyzed. Prey fish species were identified by using undigested species-specific bones and other hard remains – otoliths (sagittae); pharyngeal teeth; jaws; and chewing pads. A reference collection of fish bones as well as published morphometric statistics
and images (Härkönen 1986, Leopold et al. 2001) were used for species identification. Great Cormorant prey fish total length (TL) and weight were calculated from bone-length:fish-length and fish-length:weight relationships. Parameters for these relationships were estimated from our reference collection in most cases, supplemented by published relationships for some species (Härkönen 1986, Leopold et al. 1998, Leopold et al. 2001). A visual correction to compensate for the erosion of the sampled otoliths was applied by comparing these with otoliths of similar size from our reference collection. A correction coefficient of 1.1 was used for slightly eroded otoliths (Engström and Jonsson 2003). The Great Cormorant foraging ground was determined according to the ecological category (marine, freshwater, diadromous) of the fish indentified from the pellets and their abundance in the Curonian Lagoon and the Baltic Sea (Virbickas 2000, Gaigalas 2001, Repečka 2003a). Crustacean and molluscan shell remains retrieved from the pellets, specific for these waters, were also identified.

The proportions by numbers and biomass of the main fish species in the Great Cormorant diet during the study period were compared between years to assess inter-annual differences. Seasonal variation in diet was investigated by comparing diet composition in spring (March – May) and summer (June – August). The annual and seasonal variation of marine fish contribution in the diet was also evaluated. The proportion by weight and number of each prey fish length-group in the Great Cormorant diet was estimated for selectivity assessment. The largest fish by length and weight in the diet were identified as well. Contribution by age-group among the most important prey fish species in the Great Cormorant diet i.e. Roach *Rutilus rutilus*, Perch *Perca fluviatilis* and Ruffe *Gymnocephalus cernuus* was assessed using length-at-age data. Great Cormorant diet species preferences and Roach, Perch and Ruffe length selectivities were assessed in 2008–2010 and Jacobs’ selectivity index was used (Jacobs 1974). Scientific fishing during the summer season was implemented to determine fish community composition and fish size distribution using a set of six contiguous gillnets with different mesh sizes (14-17-21.5-21-30-33 mm, knot-to-knot). Great Cormorant diet composition data for the same season was used in the selectivity assessment. In order to evaluate direct and indirect competition between Great Cormorants and commercial fishermen, the Perch and Roach size selectivity of 40 – 45 mm mesh-size gillnets was analyzed using the scientific fishing data for the Curonian Lagoon during 2005–2010.

Muscle samples for stable isotope analysis (SIA) were collected from fish in the Curonian Lagoon and the Baltic Sea littoral area. At least three samples for each fish length group were taken, each with three individual fish in the sample. In total, 118 samples of 17 fish species were used in the analysis. Young fledgling wing feathers were used for Great Cormorant SIA. In total 37 samples were collected. Stable isotope ratio deviations from the standards $\delta^{13}C$ and $\delta^{15}N$, and the amounts of C and N in the samples were determined using continuous-flow isotope mass spectrometry (ANCA SL 20-20, PDZ Europa) at the Stable Isotope Facility, UC Davis, USA. Vienna PeeDee Belemnit for carbon and atmospheric $N_2$ for nitrogen were used as standard reference material. The linear mixing model IsoError was used for calculating isotopically distinctive food source proportions (Phillips and Gregg 2003). A 1.4 ‰ $\delta^{13}C$ isotopic discrimination factor in Great Cormorant feathers was used for modeling (Hobson 2009). C:N ratios were calculated for evaluation of lipid effect on $\delta^{13}C$. Diet composition assessed from pellets (n=75), collected during the feather growth period (May – beginning of June), was used for comparison with the modeling results. Normalization of $\delta^{13}C$ was not
applied because the estimated mean C:N ratio in fish muscle was 3.3±0.1 (and did not exceed 3.5 in any sample) indicative of a low lipid content with insignificant effect on δ\(^{13}\)C (Post \textit{et al.} 2007, Logan \textit{et al.} 2008, Abrantes \textit{et al.} 2012).

Total consumption by Great Cormorants was estimated by multiplying daily food intake from the "bird-day" number (number of cormorants per day during all season). Fish biomass consumption in the Curonian Lagoon and the Baltic Sea was calculated according to the proportions of marine and lagoon fish in the diet. Consumption of the most important fish in the diet was estimated taking into account seasonal changes in Great Cormorant abundance and diet composition. The number of Great Cormorants was assessed by counting breeding birds in the Juodkrantė colony (Ložys and Dagys 2008, J. Zarankaitė 2012, Curonian Spit National Park, \textit{pers. comm.}). Average Great Cormorant fledging success during the study period in the Juokrantė colony was 2.5 fledglings per nest (Dagys \textit{et al.} 2007, J. Zarankaitė 2012, \textit{pers. comm.}). In the assessment of prey fish species consumption we assumed that the diets of chicks and adults did not differ. The Great Cormorants’ diet after leaving the colony was considered to be the same as it was in the colony during the summer season. Great Cormorant number dynamics and phenology were evaluated according to bird counts and other monitoring data (Dagys \textit{et al.} 2004, J. Zarankaitė 2012, \textit{pers. comm.}). For consumption assessment an estimated average daily food intake of 494 g for an adult Great Cormorant, based on respirometry conducted under laboratory conditions, was used (Ridgway 2010, Schmid \textit{et al.} 1995). Daily food intake was calculated according to recommended assimilation efficiency 0.8 and an average prey energy density of 5.42 kJ·g\(^{-1}\) (Carss \textit{et al.} 1997). We used an average daily food intake of 408 g for a chick during the entire nesting period, estimated by using nest balances (Carpentier and Marion 2003).

**Ichthyological survey.** Fish community monitoring data from the Curonian Lagoon were used for evaluating of Great Cormorant long-term impact on fish populations. Monitoring was conducted at two sites – near the Nemunas River delta and near the settlement Dreverna (Fig. 1), annually in the second part of July from 1993 according to the standard method described by Thoresson (1993). Fish abundance and biomass were expressed using the standardized index - Catch Per Unit Effort (CPUE) – fish number or biomass, caught by a standard set of nets per night at one station. The spatial impact of Great Cormorants was evaluated using scientific fishing at 12 stations, located at different distances from the colony (up to 23 km) along the western coast of Curonian Lagoon (Fig. 1). Scientific fishing was carried out in July 2009 and 2010. A set of six gillnets with different mesh sizes (14-17-21.5-21-30-33 mm) was used in the scientific fishing.

Round Goby \textit{Negobius melanostomus} population expansion in the Curonian Lagoon was studied from July to September during 2007–2010. The study took place at 17 sites from the Kiaulės Nugaros Island in the northern part of the Lagoon to Parnidis Cape near the settlement Nida and at Ventė Cape in the south of the Lithuanian territory (Fig. 1). A beach seine was used for scientific fishing. Biomass and number of all fish species were estimated in the catchment area (1000 m\(^2\)).

Samples for the population parameters of the most important fish species in the Great Cormorant diet were taken with a set of 11 gillnets (mesh sizes: 14-17-21.5-25-30-33-38-45-50-60-70 mm). Relative abundance (CPUE), length distribution and sex ratio were estimated. Scientific fishing took place at 15 sites between the settlement Nida and
Nemunas River delta in the south and Klaipėda Strait in the north of the Lagoon (Fig. 1). Thirty-one instances of scientific fishing were implemented in 2009, and 23 in 2010. One thousand two hundred and seventy three (1,273) samples of Roach, Perch and Ruffe were taken during 2009, and 932 in 2010 to assess population age structure and growth. Samples of 25 males and 25 females were arbitrarily selected from length groups (2.5 cm intervals for Roach and Perch, 1 cm for Ruffe), where available. Sagittal otoliths (sagittae) were used for age determination. Annual rings in transverse otolith sections were identified and counted using a transmitted light microscope. Ages of individual fish were assigned according to the number of translucent bands alternating with opaque zones.

Figure 1. Ichthyological study sites in the Curonian Lagoon.

1 pav. Ichtiologinių tyrimų akvatorijos Kuršių mariose.
Statistical methods. A significance level of $p<0.05$ was specified a priori for all statistical analyses. Mean values are presented with their standard deviation ($\pm$SD) unless noted otherwise. Linear, polynomial and power regressions were used for prey fish length and weight calculations. T-test, one-factor ANOVA, non-parametric Mann-Whitney U and $\chi^2$ tests were used to test for differences. Jacobs’ selectivity index was used to calculate size and species preferences: $D = (r - p) / (r + p - 2rp)$, where $r =$ the proportion of the particular species or length group in the diet, and $p =$ proportion in the fish community (Jacobs 1974). Spearman correlation and linear regression were used for relationship analyses. Multivariate redundancy analysis (RDA) was applied for linking fish biomass variation to cormorant abundance and commercial landings. Square-root transformation was applied to fish community parameters data.

Results

Great Cormorant diet. Thirty-four fish species and two taxa, identified only to genus and family respectively (gobies Pomatoschistus sp. and sandeels Ammodytidae), were identified in the diet of Great Cormorants at the Juodkrante colony (Table 1). Thirteen prey fish species were found in Great Cormorant pellets annually, comprising 91.9% of the Great Cormorant diet by biomass. Cyprinids and percids were the most important fish in the Great Cormorant diet, comprising 21% and 62.1% by numbers, and 47.3% and 38% by biomass respectively. The remains of four crustacean species were also found in Great Cormorant pellets: Common Shrimp Crangon crangon, the isopod Saduria entomon, Chinese Mitten Crab Eriocheir sinensis, and Spiny-cheek Crayfish Orconectes limosus.

Figure 2. Frequency of occurrence of the most important species and different ecological groups of Great Cormorant prey found in pellets at the Juodkrantė colony in 2005–2010.


The frequency of occurrence of the three dominant species combined in the Great Cormorant diet exceeded 60%, comprising Ruffe 80.4%; Roach 45.9%; and Perch 68.5%. The frequency of occurrence of five other prey species combined exceeded 10%
The frequency of occurrence of the Round Goby increased considerably during the study period; identified for the first time in 2007, it reached 21.6% in 2009–2010. Overall, 28,180 prey fish items were identified in the sample of 1,032 pellets. Numbers of prey per pellet varied from 1 to 162 (mean 27.7). Three species were the most abundant by numbers (Fig. 3); Ruffe (40.4%), Perch (20.5%), and Roach (16.9%), contributing 77.7% in the diet. Smelt *Osmerus eperlanus* was the more abundant among the other prey, contributing 8.8% by numbers. Other prey fish species in the diet reached 4% by number.

Three fish species were the most important by biomass (Fig. 3), Roach (37%), Perch (16.2%), and Ruffe (17.2%), comprising 70.3% in the diet. Pikeperch *Sander lucioperca* was 4.6% in the diet and other species were less than 4%.

The frequency of occurrence of marine fish remains in pellets during the study period was 20.1%, compared with 94% freshwater and diadromous fish (Fig. 2). Marine feeding contributed 9.4% by biomass. Marine fish as a proportion in Great Cormorant diets during the chick feeding period, was 16.5±4.4% (±SE) when estimated using δ¹³C in a two sources mixing model. Marine fish contribution in the diet by weight, based on pellet analysis during the same period, was 17.7%.

![Figure 3. Diet composition of the Great Cormorant by numbers and biomass at the Juodkrantė colony in 2005–2010.](image-url)

3 pav. Juodkrantės kolonijoje perinčių didžiųjų kormoranų mitybos svarbiausių žuvų dalis racione pagal skaičių ir masę (2005–2010 m.).
Table 1. Diet composition of the Great Cormorant at the Juodkrantė colony during 2005–2010 (*regurgitated fish).

<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>Proportion in the diet, %</th>
<th>Mean</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>By biomass</td>
<td>By numbers</td>
<td>Frequency of occurrence, %</td>
</tr>
<tr>
<td>1</td>
<td>Atlantic herring Clupea harengus</td>
<td>0.5</td>
<td>1.5</td>
<td>4.9</td>
</tr>
<tr>
<td>2</td>
<td>Twaitie Shad Alosa fallax</td>
<td>&lt;0.1</td>
<td>0.6</td>
<td>1.1</td>
</tr>
<tr>
<td>3</td>
<td>Sprat Sprattus sprattus</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.6</td>
</tr>
<tr>
<td>4</td>
<td>Sea Trout Salmo trutta</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.6</td>
</tr>
<tr>
<td>5</td>
<td>Smelt Osmerus eperlanus</td>
<td>8.8</td>
<td>2.8</td>
<td>34</td>
</tr>
<tr>
<td>6</td>
<td>European Eel Anquilla anquilla</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>7</td>
<td>Pike Esox lucius</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.3</td>
</tr>
<tr>
<td>8</td>
<td>Roach Rutilus rutilus</td>
<td>16.9</td>
<td>37</td>
<td>75.9</td>
</tr>
<tr>
<td>9</td>
<td>Bream Abramis brama</td>
<td>2</td>
<td>3.5</td>
<td>27.8</td>
</tr>
<tr>
<td>10</td>
<td>Smelt Osmerus eperlanus</td>
<td>8.8</td>
<td>2.8</td>
<td>34</td>
</tr>
<tr>
<td>11</td>
<td>Tench Tinca tinca</td>
<td>&lt;0.1</td>
<td>0.4</td>
<td>0.7</td>
</tr>
<tr>
<td>12</td>
<td>Common Carp Cyprinus carpio</td>
<td>&lt;0.1</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>13</td>
<td>Bleak Alburnus alburnus</td>
<td>0.2</td>
<td>1.1</td>
<td>3.4</td>
</tr>
<tr>
<td>14</td>
<td>Ruffe Gymnocephalus cernuus</td>
<td>0.2</td>
<td>1.3</td>
<td>3.2</td>
</tr>
<tr>
<td>15</td>
<td>Perch Perca fluviatilis</td>
<td>1.6</td>
<td>1.9</td>
<td>5.6</td>
</tr>
<tr>
<td>16</td>
<td>Three-spined Stickleback Gasterosteus aculeatus</td>
<td>6.3±0.5</td>
<td>1.7±0.6</td>
<td>6.9</td>
</tr>
<tr>
<td>17</td>
<td>Shorthorn Sculpin Myoxocephalus scorpius</td>
<td>&lt;0.1</td>
<td>0.3</td>
<td>0.5</td>
</tr>
<tr>
<td>18</td>
<td>Perch Perca fluviatilis</td>
<td>20.5</td>
<td>16.2</td>
<td>68.5</td>
</tr>
<tr>
<td>19</td>
<td>Pike Sander lucioperca</td>
<td>1.3</td>
<td>4.6</td>
<td>20.6</td>
</tr>
<tr>
<td>20</td>
<td>Flounder Platichthys flesus</td>
<td>0.6</td>
<td>0.2</td>
<td>3.5</td>
</tr>
<tr>
<td>21</td>
<td>Gobiid Gobius niger</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>22</td>
<td>Turbot Psetta maxima</td>
<td>0.2</td>
<td>0.3</td>
<td>1.1</td>
</tr>
</tbody>
</table>
The mean total length (TL) of fish found in pellets was 9.4 ± 4.2 cm (TL) and the mean weight 15.4 ± 31.9 g. Small prey fish dominated the diet of Great Cormorants at the Juodkrantė colony, with 82.8% in the 12 cm or smaller length group, comprising 33.8% of the diet by weight (Figure 4). The largest identified fishes were Burbot *Lota lota* of 40.1 cm and 466.3 g, European Eel *Anguilla anguilla* of 39.1 cm and 101.5 g, Pikeperch of 37.1 cm and 446 g, and Tench *Tinca tinca* of 35.1 cm and 699.2 g (Table 1). The majority of the most important Great Cormorant prey fish were young and from the smaller length groups. Roach 1–4 years in age in the 4–16 cm length group represented 83.1% of species found in pellets. The faster growing Perch, identified in pellets, fish of 2–10 cm length group and 1–2 years old comprised 79.5% by numbers. Commercial size Perch (>18 cm, TL), three years and older, comprised 2.1% in the diet by number, commercial size Roach (same size, five and years old) – 12.7%. Selectivity results for Great Cormorant diet and commercial 40–45 mm mesh gillnet fishing showed little direct competition. Roach eight-years and older, and Perch 5–6 years old that were more than 25 cm long, dominated catches in gillnets. Perch of this size comprised 80% of the perch in catches, whereas in the Great Cormorant diet only 0.2% by number. Roach of 25 cm and larger comprised 90.8% of the Roach in the gillnets and 2% in Great Cormorant diet. Accordingly, the Perch share in the diet by biomass was 4.7%, whereas Roach was more important and shared 17%.

Length distributions of Roach, Perch and Ruffe in Great Cormorant diets and scientific fishing catches differed in most instances during 2008–2010. Generally, small-sized fish were proportionally more abundant in the Great Cormorant diet than in the Curonian Lagoon fish community. Great Cormorants consumed a larger proportion of 9–10 cm Ruffe (except in 2008, when for all length groups up to 15 cm frequencies were similar), 10–11 and 14–17 cm length Perch, and Roach smaller than 18 cm than the ratios observed in the Lagoon. Scientific fishing in the Curonian Lagoon showed that catches and Great Cormorant diet fish species composition by numbers were different in 2008–2010 ($\chi^2=27.4$, $p<0.0001$, df=4) (Fig. 5). Perch (except in 2009, when proportions were similar), Roach and Pikeperch were more common in the Great Cormorant diet than in scientific catches, while Ruffe and White Bream *Blicca bjoerkna* (except in 2008, when proportion in the diet was somewhat less) were caught less frequently by Great Cormorants (Table 2). Great Cormorant prey fish species, from diet preference investigation, contributed 91.8–96.5% of the diet by numbers among fish, caught in the Lagoon, and 93.6–95.7% in scientific fishing catches.
Figure 4. Distribution by length class (TL) of Great Cormorant prey fish numbers and biomass.

4 pav. Didžiųjų kormoranų atrajose identifikuotų žuvų pasiskirstymas ilgio (TL) grupėse pagal skaičių ir masę.

Figure 5. Great Cormorant diet and scientific fishing in the Curonian Lagoon catches composition by numbers in 2008–2010.

5 pav. Didžiojo kormorano raciono ir mokslinių žvejybų Kuršių mariose laimikų sudėtis pagal skaičių 2008–2010 m.
Great Cormorant diet composition varied significantly during the study period in 2005–2010 both by numbers and biomass (Fig. 6). The proportion of Ruffe ranged from 31.3 to 50.5% by numbers and from 8.2 to 28% by biomass. Roach proportions in the diet ranged from 10.5 to 25.1% by numbers and from 23.2 to 51.3% by biomass. Perch
comprised 8.7 – 31.6% by numbers and 10.2 – 21.6% by biomass in the diet. These three prey fish species dominated the diet during the entire study period and their proportion when combined ranged from 65.7 to 86.5% by numbers and from 61.2 to 81.1% by biomass. The proportion of marine fish varied about four-fold, comprising 3 –11.9% by numbers and 3.2 –14.3% by biomass. Marine fish as a proportion of the diet during the period of 2009–2010 exceeded average values over the entire study period and comprised 14.3% by numbers and 12.3% by biomass. The frequency of occurrence of marine fish ranged about two-fold, comprising 3 –11.9% by numbers and 3.2 –14.3% by biomass. Marine fish as a proportion of the diet varied significantly both by numbers ($\chi^2=31.7$, df=4, p<0.0001) and biomass ($\chi^2=12.1$, p=0.0164, df=4) during the duration of the study period, except for the composition by biomass in 2005 ($\chi^2=4$, p=0.4, df=4) (Fig. 7).

Table 2. Fish proportions by numbers in Great Cormorant diet and scientific fishing catches and species preferences in the Curonian Lagoon (2008–2010, summer). Jacobs’ selectivity index value 1 shows complete preference, –1 complete avoidance, and 0 no preference.

<table>
<thead>
<tr>
<th>Species</th>
<th>2008 Diet</th>
<th>2008 Lagoon</th>
<th>Jacobs' index</th>
<th>2009 Diet</th>
<th>2009 Lagoon</th>
<th>Jacobs' index</th>
<th>2010 Diet</th>
<th>2010 Lagoon</th>
<th>Jacobs' index</th>
<th>Mean Diet</th>
<th>Mean Lagoon</th>
<th>Jacobs' index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruffe</td>
<td>0.22</td>
<td>0.51</td>
<td>0.57</td>
<td>0.19</td>
<td>0.19</td>
<td>0.57</td>
<td>0.33</td>
<td>0.33</td>
<td>-0.31</td>
<td>0.48</td>
<td>0.48</td>
<td>-0.31</td>
</tr>
<tr>
<td>Perch</td>
<td>0.09</td>
<td>0.16</td>
<td>0.15</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.15</td>
<td>0.15</td>
<td>0.15</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td>Roach</td>
<td>0.50</td>
<td>0.52</td>
<td>0.45</td>
<td>0.32</td>
<td>0.32</td>
<td>0.32</td>
<td>0.27</td>
<td>0.27</td>
<td>0.27</td>
<td>0.12</td>
<td>0.12</td>
<td>0.12</td>
</tr>
<tr>
<td>White Bream</td>
<td>0.12</td>
<td>0.10</td>
<td>0.08</td>
<td>0.13</td>
<td>0.13</td>
<td>0.13</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.07</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>Pikeperch</td>
<td>0.02</td>
<td>0.01</td>
<td>0.22</td>
<td>0.08</td>
<td>0.08</td>
<td>0.22</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
</tr>
</tbody>
</table>

Great Cormorant prey fish consumption. The size of the Great Cormorant breeding population at the Juodkrantė colony varied from 2,362 to 3,367 pairs during the study period. One cormorant pair with chicks consumed 247.1 kg fish per year. Total consumption by Great Cormorants in the colony, ranged from 583.7 to 824.4 t fish biomass per year during 2005–2010 (mean 729.2±86.1 t), of which 568.3–728.6 t (mean 653.3±59.4 t) of fish were taken from the Curonian Lagoon. Among the most important prey fish species, the largest biomass consumed was of Roach (270.7 t per year), Ruffe (121.8 t) and Perch (117.8 t), with the total consumption of these species of 510.3 t per year accounting for 77.8% of all biomass consumed. Among the other prey fish species, considerable consumption of Pikeperch (36.1 t), Flounder Platichthys flesus (26.9 t), White Bream (25.7 t) and Bream Abramis brama (20.6 t) occurred. Great Cormorants also consumed large quantities of Round Goby, amounting to 36 t per year during the period after 2007 when it was first discovered in the diet. Consumption of other fish species did not exceed 20 t per year. Commercially targeted fish species comprised 76.9% (561.9 t) of all consumed biomass, 26.7% of these were of commercial size,
mostly Roach (18.8%), Perch (4.3%) and smelt (2.4%). Most of the fish consumed were low-priced (average wholesale price for fresh fish less than 3.5Lt/kg (approx. 1 EUR)), mostly Roach, Perch and White Bream (Fig. 8). Only a few individuals of high value species e.g. European Eel, and Sea Trout Salmo trutta trutta, were identified in Great Cormorant pellets, comprising less than 0.05% of consumed biomass. Average consumption of medium- and high-priced fish species was 63 t per year, mostly Pikeperch and Smelt. Average fish consumption from the Curonian Lagoon by Great Cormorants from the Juodkrantė colony, reached 15.8±1.4 kg during 2005–2010. Average commercial landings for the same period were 26.9 kg/ha per year in the Lithuanian part of the Lagoon (Table 3). Compared to commercial catches in the Lagoon, Great Cormorants consumed more Perch (117.8 t consumption and 47.7 t average landings), but relatively less White Bream (25.7 and 29.6 t respectively) and Roach (270.7 and 366.5 t respectively). Biomass of the other fish, taken by Great Cormorants was much less than commercial landings of those species. Great Cormorant took 7.1% of the total fish biomass in the Lithuanian part of the Lagoon during 2008–2010 (Repečka 2009, 2010). Ruffe consumption was the highest and amounted to 24.9% of total Ruffe biomass in the Lagoon. Proportions of consumed Perch and Roach biomass exceeded average levels and were 11.8 and 9.1% accordingly (Table 3).

Table 3. Consumption and average landings of the most important fish in the Great Cormorant diet and commercial fishery in 2005–2010 and their average biomass in the Lithuanian part of the Curonian Lagoon in 2008–2010 (Repečka 2009, 2010).

<table>
<thead>
<tr>
<th>Species</th>
<th>Cormorant consumption</th>
<th>Commercial landings</th>
<th>Cormorant consumption and commercial landings ratio</th>
<th>Biomass</th>
<th>Cormorants consumed biomass, %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>kg/ha</td>
<td>t</td>
<td>kg/ha</td>
<td>t</td>
</tr>
<tr>
<td>Roach</td>
<td>270.7</td>
<td>6.5</td>
<td>366.5</td>
<td>8.8</td>
<td>0.7</td>
</tr>
<tr>
<td>Bream</td>
<td>20.6</td>
<td>0.5</td>
<td>350.7</td>
<td>8.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Vimba</td>
<td>7.7</td>
<td>0.2</td>
<td>105.7</td>
<td>2.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Pikeperch</td>
<td>36.1</td>
<td>0.9</td>
<td>84.7</td>
<td>2.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Perch</td>
<td>117.8</td>
<td>2.8</td>
<td>47.7</td>
<td>1.1</td>
<td>2.5</td>
</tr>
<tr>
<td>Smelt</td>
<td>17.0</td>
<td>0.4</td>
<td>34.8</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>White Bream</td>
<td>25.7</td>
<td>0.6</td>
<td>29.6</td>
<td>0.7</td>
<td>0.9</td>
</tr>
<tr>
<td>Ruffe</td>
<td>121.8</td>
<td>2.9</td>
<td>8.7</td>
<td>0.2</td>
<td>14.0</td>
</tr>
<tr>
<td>Other</td>
<td>35.9</td>
<td>0.9</td>
<td>87.7</td>
<td>2.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>653.3</td>
<td>15.7</td>
<td>1115.8</td>
<td>26.9</td>
<td>0.6</td>
</tr>
</tbody>
</table>
Great Cormorant impact on spatial fish distribution. Fish abundance and biomass in the catches from the scientific fishing did not differ between years 2009 and 2010 (t test; abundance: t=0.90, p=0.38; biomass: t=0.48, p=0.64; d.f.=22). Three fish species dominated these catches – Ruffe, Roach and Perch, comprising 84.6% (58.6–96.7%) by numbers and 73.5% (43.5–95.6%) by biomass in 2009 and respectively 88.4% (63.5–98.5%) and 70.1% (38–89.1%) in 2010. Proportions of Roach and Ruffe in the catches changed substantially during the study period: the proportion of Roach decreased (27.1% and 10.7% by numbers, 33.4% and 16.8% by biomass) and the proportion of Ruffe – increased (41.1% and 66.8% by numbers, 14.8% and 29.1% by biomass). The proportion of Perch varied less (16.3% and 10.8% by numbers, 25.4% and 24.1% by biomass) than the other species.

Substantial differences between study sites were observed in 2009 and 2010, according to both the total fish abundance and biomass. Even larger differences (up to 1–2 orders of magnitude) were observed in the abundance of the most important among the species, Roach, Ruffe and Perch in the fish community. The total abundance of fish, as well as the abundance and biomass of the most important fish species, differed significantly between study sites in both years. Total fish biomass at the same site did not differ between years ($\chi^2$ test; $\chi^2=16.43$, p=0.126, d.f.=11). Total fish abundance (CPUE) correlated negatively with increasing distance from the Juodkrantė cormorant colony (Table 4). The negative form of this relationship remained the same in both study years, although it was stronger in 2009 (Spearman correlation, r=−0.73). Fish biomass in 2009 also correlated negatively, including Ruffe, Roach and Perch biomass and abundance. Total fish abundance and biomass relationships with distance from the colony were weak in 2010, although for Ruffe the negative correlation remained. The relationship of Perch abundance and biomass with distance changed in 2010 to correlate positively (accordingly r=0.52 and r=0.22). Changes in Roach abundance and biomass were of similar pattern, although were less pronounced (Fig. 9).
Correlation of fish abundance and biomass with distance from the Great Cormorant colony was statistically significant \( (p<0.05) \) for only three instances – abundance and biomass of all fish and Roach abundance which correlated negatively in 2009.

Figure 9. Abundance of Perch, Roach and Ruffe in relation to the distance from the Juodkrantė cormorant colony in 2009–2010.

9 pav. Ešerio, kuojos ir pūgžlio gausumas (CPUE) priklausomai nuo atstumo atstumo iki Juodkrantės kormoranų kolonijos 2009–2010 m.
Table 4. Spearman’ correlations of the distance from the Juodkrantė cormorant colony with fish abundance and biomass in the Curonian Lagoon in 2009–2010. Statistically significant (p<0.05) values are in bold.

<table>
<thead>
<tr>
<th></th>
<th>Abundance</th>
<th>Biomass</th>
<th>Abundance</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>–0.73</td>
<td>–0.59</td>
<td>–0.11</td>
<td>–0.09</td>
</tr>
<tr>
<td>Perch</td>
<td>–0.28</td>
<td>–0.19</td>
<td>0.52</td>
<td>0.22</td>
</tr>
<tr>
<td>Roach</td>
<td>–0.45</td>
<td>–0.36</td>
<td>–0.18</td>
<td>–0.24</td>
</tr>
</tbody>
</table>

Long-term impact of Great Cormorant predation on fish populations and their community in the Curonian Lagoon. Average fish biomass and abundance in scientific fishing catches did not change during the entire fish community monitoring period (1993–2011) in the Curonian Lagoon (linear regression; biomass: $r^2=–0.05$, $F=0.17$, $p=0.68$; abundance: $r^2=–0.05$, $F=0.13$, $p=0.73$), although it fluctuated substantially (Fig. 10). Relative fish biomass (CPUE) differed more than three-fold among the years ranging from 18.1 to 52.2 kg.

![Figure 10. Fish biomass and abundance (CPUE) in the Curonian Lagoon according to monitoring catches in 1993–2011.](image-url)
Both fish biomass and abundance were higher at the Atmata site (southern part of Lagoon) than near Dreverna (northern part of Lagoon) and the differences were statistically significant (ANOVA; biomass: $F_{2,38}=573.4$, p<0.01, abundance: $F_{2,38}=618.3$, p<0.01). Fish biomass and abundance at the Atmata were 35.6±17.7 kg and 478±230 individuals per unit of effort respectively, and 25.9±12.9 kg and 394±230 at the Dreverna site. Roach, Perch and Ruffe dominated the monitored catches at both sites. Their total proportion by biomass was 65.6±17.4% at Atmata and 77.1±13.1% at Dreverna. Total fish, as well as the most important Great Cormorant prey fish, biomass and abundance did not change in both monitoring sites (linear regression; p>0.5). Only

Figure 11. RDA triplot for fish biomass (Gymno_B - Ruffe, Perca_B - Perch, Rutil_B - Roach, Other_B – other fish ir Tot_B - total) in the monitoring catches with Great Cormorant numbers (Phala) and commercial landings (Land – total landings, Rutil_L – Roach landings, Perc_L – Pech landings) in the Curonian Lagoon in 1993–2010 as explanatory variables. Monitoring site (station) and period (1993–2000 and 2001-2011) used as nominal variables.
an increase in Roach biomass at Atmata was statistically significant (linear regression; \( r^2=0.04, F=7.17, p<0.01 \)). The relationship between Great Cormorant numbers and fish biomass was weak and not significant statistically at both monitoring sites (linear regression; \( p>0.47 \)). Increases in Great Cormorant numbers explained less than 1% of the variation in biomass of the most important cormorant prey fish species, Roach, Perch and Ruffe, at Atmata and Dreverna, although regressions were not significant statistically (\( p>0.19 \)), except Roach at Atmata (linear regression; \( r^2=0.03, F=5.63, p=0.02 \)). Redundancy analysis (RDA) did not show more substantial impacts by either cormorants or the commercial fishery on the total fish biomass and the biomass of the most important Great Cormorant prey fish in the monitoring catches (1993–2010) (Fig. 11). These factors explained 17% of fish biomass variation (\( p=0.001 \)).

The breeding population of Great Cormorants at the Juodkrantė colony increased in size from 195 to 3,808 pairs from 1993 to 2011. Consumption of fish biomass by cormorants in the Curonian Lagoon increased from 45 t in 1993 to 729 t in 2010. The increase in Great Cormorant consumption (more than 600 t) was similar to that of commercial catches during the same period (except 2009–2010). Commercial landings in the Lithuanian side of the Lagoon increased from 549–652 t per year in 1993–1995 to an average of 1230 t in 2000–2008 and decreased by a quarter from 2009, following a reduction in fishing effort.

**Invasive Round Goby in the Great Cormorant diet.** A gradual increase in Round Goby abundance and its progressive expansion within the Curonian Lagoon in a southerly direction from Klaipėda Port was observed during surveys in 2007–2010. The Round Goby was found in beach seine catches near Juodkrantė in 2007 and at Ventė Cape in 2010. Sites with high abundance (>10 individuals in 1000 m\(^2\)) of Round Goby were registered further southward during the study period – near Alksnynė (Site No. 3, Fig. 1) in 2007 and at Avikalnio Cape (Site No. 8) in 2010. The highest abundances were found at Lybio Cape (Site No.5, 75 ind., 0.6 kg 1000 m\(^2\)) and near the cormorant colony (Site No. 7, 251 ind., 0.8 kg 1000 m\(^2\)) in 2009. Round Goby comprised 51.3% and 46.8% of total fish biomass in the respective beach seine catches.

Round Goby was found in Great Cormorant diets in 2007 for the first time, comprising 0.6% by number and 0.3% by biomass. It’s importance in the Great Cormorants’ diet increased during the following years. Round Goby as a proportion of the diet was 8.7% by biomass (the fourth dominant prey fish) and the total biomass consumed by Juodkrantė colony cormorants was 70.6 t in 2010 (Fig. 12). The importance of the Round Goby in the Great Cormorant diet varied seasonally, with a greater proportion observed in spring. The proportion by biomass in spring 2009 was 9% and in summer it was 6%; and 10.2% and 7% for the respective seasons in 2010. Most of the round gobies (73.4–90%), identified in Great Cormorant pellets, were caught in the Baltic Sea. The importance of the marine feeding increased following the Round Goby population expansion. Marine fishes comprised 7.5% by biomass in the Great Cormorant diet during 2005–2008, whereas round gobies increased this proportion to 13.3% in 2009–2010.
Discussion

**Great Cormorant diet.** Great Cormorant diet composition, both qualitatively and quantitatively, is one of the most important parameters for assessing the impact of cormorants on fish communities. Pellet analysis, used in our study, like other conventional diet investigation methods, has some limitations (Carss *et al.* 1997, Barrett *et al.* 2007). Compensating for the biases of otolith erosion in fish weight calculations, and otolith size correction were applied in our study. However, alternative quantitative diet investigation methods are required for evaluating correction reliability, such as stable isotope composition analysis. Proportions of isotopically different food sources can be assessed by applying mixing models (Hobson 2009). Great Cormorant prey fish analysis showed high isotopic variability. Salinity gradients are among the factors determining differences in stable isotope composition (Bearhop *et al.* 1999, Fry 2002, Russel *et al.* 2003a). Curonian Lagoon and Baltic Sea fishes differed according to $\delta^{13}$C, allowing us to use a two sources mixing model for calculating the ratios of these food components. Marine and freshwater fish proportions in the Great Cormorant diet estimated by the mixing model were very close to the results from pellet analysis. These results show that pellet analysis can be used effectively in qualitative cormorant diet analysis.

The Great Cormorant Juodkrantė colony is located close to the Baltic Sea as well as the Curonian Lagoon, water bodies with high fish diversity. Those fish species, considered to be the most common (Repečka 2003a) were found in Great Cormorant diets during this long term study (Table 1). The most important Great Cormorant prey fish species, Roach, Ruffe and Perch, dominated in scientific fishing catches and diet,
comprising 70.3% and 71.8% respectively. These same species are dominating the diets of Great Cormorants feeding in many of the fresh and brackish waters of Europe (De Nie 1995, Van Dobben 1995, Suter 1997, Carss 2003, Engström and Jonsson 2003, Mous et al. 2003, Stempniewitzcz et al. 2003a, Carss and Marzano 2005, Lehikoinen 2005, Čech et al. 2008). They also often comprise a large proportion of the diets of Great Cormorant populations engaged in social fishing (Van Eerden and Voslamber 1995). The main feeding area for Great Cormorants from the Juodkrantė colony was Curonian Lagoon. Fish caught in the Lagoon comprised 90.6±3.8% in the Great Cormorants’ diet by biomass. Curonian Lagoon is a highly productive water body, with a fish biomass reaching 200–230 kg/ha (Repečka 2007, 2009, 2010). Fish abundance in scientific catches differed ten-fold, and CPUE in Curonian Lagoon and the Baltic Sea coastal area adjacent to Curonian Spit were 91.1 and 8.9 respectively (Ložys 2008). Lower fish abundance can explain less effective feeding in the sea. The frequency of pellets containing the remains of marine fish (together with mixed pellets, containing remains from both marine and freshwater fish) was 20.1%, although the proportion of marine fish in the diet was 7.5% by number. Great Cormorants feed in shallow coastal waters up to 20 m depth (Van Eerden et al. 1995). The Baltic Sea coastal area that is within this depth range, rendering it accessible to cormorants from the Juodkrantė colony, is much smaller than the accessible area within Curonian Lagoon. Social fishing is another factor that might explain the Lagoon’s importance for Great Cormorant feeding. Shallow turbid water and a large cormorant colony exceeding 1000 breeding pairs are essential conditions for social fishing (Van Eerden and Voslamber 1995). This feeding strategy allows substantially increased foraging efficiency (Van Eerden et al. 2003).

In general, Great Cormorants took small fish in higher proportions than they occurred within the fish community of Curonian Lagoon. The Great Cormorants’ diet was positively selective towards smaller rather than commercial sized (18 cm TL) Roach and Perch, and smaller than 11 cm length Ruffe. Although Great Cormorants can swallow quite large fish, the extent of their direct competition with the commercial fishery in the Lagoon is low. Contrary selectivity tendencies were identified in an analogous study at Lake Ymsen (Sweden): in general, Great Cormorants selected larger fish than in Curonian Lagoon (Engström and Jonsson 2003) and they differed in their prey species preferences. The Lake Ymsen and Curonian Lagoon have many similarities: they are large, shallow, eutrophic, turbid, water bodies with similar fish community compositions. Different cormorant feeding strategies may explain the diet selectivity differences between these water bodies. Although common in Curonian Lagoon, social fishing is impossible in the Lake Ymsen because the Great Cormorant colony is too small to create a large feeding flock, despite other conditions being suitable (Van Eerden and Voslamber 1995).

Substantial seasonal variation in Great Cormorant diet composition was observed in the Juodkrantė colony during the study. Proportions of the most important prey fish species in the spring and summer diet differed by more than two-fold (more than 15-fold for smelt). The intensity of cormorant pressure on fish populations may fluctuate during the year because of variation in diet composition and seasonal dynamics in cormorant abundance. In addition, young-of-the-year fish comprise a substantial proportion in the cormorant diet from the middle of summer. For example, 80% of Perch identified in pellets in the end of July–beginning of August 2010 were young-of-the-year up to 6 cm length.
**Great Cormorant prey fish consumption.** The daily food intake of 494 g used in our study for adult Great Cormorants, based on respirometry (Schmid et al. 1995, Ridgway 2010) is close to maximum values. Notably, the mean fresh weight of fish, identified in one pellet at the Juodkrantė colony, was similar – 459.1±73.1 g. Average fish consumption in 2005–2010 from the Lithuanian part of Curonian Lagoon amounted a somewhat more than half of the commercial landings. Curonian Lagoon is a highly productive water body where fish biomass exceeds 200 kg/ha (Repečka 2009, 2010). Fish production may exceed 100 kg/ha per year (Mous et al. 2003). Thus Great Cormorants consume approximately one sixth of the total fish production in the northern part of the Lagoon. Perch consumption was in contrast to the other important commercial fish species. Consumption of this species exceeded commercial catches more than two-fold. Although commercially targeted fish species comprised a major proportion in the Great Cormorant diet, the direct competition with fisherman was low. Commercial-sized fish comprised more than one quarter of the diet by weight, predominantly of low market-value Roach. Only a small extent of overlap in selectivity was found between Great Cormorants and 40–45 mm mesh size commercial gillnets. Fish larger than 25 cm (TL) dominated (80–90.8%) the commercial net catches by number, whereas these sizes were sparse in the cormorant diet (0.2–2%). Only one European Eel, the most valuable commercial fish in Curonian Lagoon, was identified among Great Cormorant pellets during the study period. Only a few regurgitated Eels have been found in the Juodkrantė colony since 1998, although the colony was visited at least a few times per month (J. Zarankaitė 2012, pers. comm.).

**Great Cormorant impact on spatial fish distribution.** The Great Cormorant colony near Juodkrantė, re-established in 1989 (Stanevičius and Paltanavičius 1997) after an exponential growth period, has stabilized and its abundance has been fluctuating around 3000 breeding pairs since 2003 (Ložys and Dagys 2008, J. Zarankaitė 2012, pers. comm.). Little is known about the mechanisms determining a stable colony size. Ashmole (1963) raised a hypothesis that large sea bird colonies might be regulated during their breeding season by depleting fish resources close to their colonies. Evidence supporting this hypothesis has only been found for a few bird species (Birt et al. 1987, Gaston et al. 2007). Only a few studies have found that cormorant predation can create Ashmole’s halo - zone of food depletion in the vicinity of their breeding colonies (Birt et al. 1987, Stempniewicz et al. 2003a). There is no evidence, however, that such decreases in fish density can regulate cormorant colonies. Moreover, cormorants are a most effective marine predator and their colonies are highly productive, even in arctic regions with scarce fish resources (Gremillet et al. 2004). Ichthyological surveys in Curonian Lagoon during 2009–2010 did not reveal any decreases in fish abundance and biomass in the vicinity to the Great Cormorant colony. Moreover, the largest fish abundances were observed in those study sites that were located close to the colony, and remained consistently so throughout the study period (Fig. 9). Spatial fish distribution survey results suggest that food resources are not a limiting factor for the Juodkrantė colony cormorants. High fledging success rates, 2.5 fledglings per nest (Dagys and Ložys 2007, J. Zarankaitė 2012, pers. comm.), indicate that food resources were plentiful.
Long-term impact of Great Cormorant predation on fish populations and their community in the Curonian Lagoon. Long-term fish community monitoring data were used for Great Cormorant impact assessment. The monitoring was implemented during 1993, the early Juodkrantė colony establishment period, when cormorant population abundance was low. Hence, monitoring data should reflect possible long-term Great Cormorant predation effects on fish community composition and population abundance. Substantial fluctuations (up to three-fold) in fish biomass and abundance were observed during this monitoring period. Total fish abundance and biomass decreased slightly overall, but the changes were not significant statistically. Long-term changes in the abundance and biomass of the most important Great Cormorant prey fish i.e. Roach, Perch and Ruffe, were also negligible.

Curonian Lagoon is a complex open water system. Changing anthropogenic and natural factors influence the fish community in the Lagoon and may cause long-term changes in biomass and community structure. The commercial fishery is one of the strongest anthropogenic factors influencing the fish community in the Lagoon. Commercial landings in Curonian Lagoon have increased during the monitoring period at a similar rate to that of fish consumption by the growing Great Cormorant population from the Juodkrantė colony. Despite their similarity in the rate of change in impact intensity, the effects of the fishery and cormorants differ. The commercial fishery targets large, mature fish, decreasing the spawning stock biomass which may reduce future stock recruitment. Cormorants mostly prey on small juvenile fish, for which mortality is largely density dependent. Hence, mortality caused by predators, is likely to be compensatory for small young fish and additive for large fish (Allen et al. 1998). Many studies have demonstrated that mortality caused by predators, or other factors, can be compensated to a particular level. Compensation mechanisms might be an important factor for the population regulation of cormorant prey fish (Dalton et al. 2009). Eutrophication is another important anthropogenic factor influencing fish biomass and population structure (De Nie 1995, Engström 2001a, Lappalainen 2002, Carpentier et al. 2003). Decreasing eutrophication is alleged as one of the factors inducing fish biomass decreases in Curonian Lagoon (Ádiers et al. 2006).

Predation on protected fish species is another aspect of cormorant impact on fish communities. Cormorants are basically opportunistic feeders, so protected species usually comprise only a small proportion in the diet because they are in low abundance. Three fish species of community importance, that are included in Habitats Directive Annex II, were identified among Great Cormorant pellets: Twaite Shad *Alosa fallax*, asp *Aspius aspius* and Sichel *Pelecus cultratus*. They comprised 1.3% by biomass in the diet which is a negligible portion.

Invasive Round Goby in the Great Cormorant diet. Round gobies were identified in the Great Cormorant pellets for the first time in 2007, and in just a few years became one of the most important prey fish species (Fig. 12). The Round Goby, originating from the Ponto-Caspian region, is rapidly expanding in the North American Great Lakes and in the European Baltic Sea regions (Corkum et al. 2004). Cormorants are perceived as problem in all of these regions. The Round Goby is a relatively small, up to 25 cm length, slow moving, benthic fish, that is easily caught by cormorants and is becoming one of their most important prey (Johnson et al. 2000, Bzoma and Meissner 2005, Bur et al. 2007, Johnson and McCullough 2008). In Lithuania, the Round Goby was first
discovered in the Baltic Sea near the Klaipėda Strait during 2002, (Bacevičius 2003, Zolubas 2003). It later spread rapidly northwards, becoming a dominant fish species in some locations (D. Daunys 2011, Klaipėda University, pers. comm.; R. Repečka 2011, Nature Research Center, pers. comm.). Expansion was slower southwards in the Baltic Sea coastal waters and in the Curonian Lagoon, where round gobies were observed in the Russian part of the Lagoon during the latter years (T. Golubkova 2011, AtlantNIRO, pers. comm.). Considerable changes in the feeding of Great Cormorants from the Juodkrantė colony might be related to the Round Goby population expansion. Most round gobies that were identified in Great Cormorant pellets were caught in the Baltic Sea. The importance of marine feeding increased nearly two-fold, approximately in proportion to the increase in the abundance of round gobies. Cormorant foraging efficiency in the sea also increased during the same period. Changes in the frequency of pellets containing marine fish were insignificant, with 20.6% in 2005–2007 and 19.5% in 2008–2010, whereas the proportion of marine fish in the pellets nearly doubled, from 6.9 to 12% between these respective periods. This increase in foraging efficiency in the sea is doubtless related to the Round Goby spreading from the Klaipėda port area toward the Juodkrantė cormorant colony and indicates that the goby is an attractive food source for Great Cormorants. Great Cormorants showed their ability to adapt effectively to a changing environment and to exploit new fish resources. Increasing importance of invasive fish species in the cormorant diet may change their ecological role. There is no evidence however, that cormorants are having a substantial impact on Round Goby populations despite their considerable consumption of this invader. On the other hand, abundant alien fish populations may have a positive effect on cormorants. For example, increases in the numbers of Great Cormorants wintering in the Gulf of Gdansk is related to the high abundance of round gobies that now exist in the Gulf (Bzoma and Meissner 2005).

Conclusions

1. Substantial diversity was characteristic of Great Cormorants’ diet at the Juodkrantė colony. Thirty-four fish species and two taxa that could not be identified to species were found in the diet. Three fish species were the most important by biomass, Roach (37%), Ruffe (17.2%) and Perch (16.2%), comprising a total of 70.3% of the diet.
2. Great Cormorant diet composition differed between years and seasons (spring and summer). The most important fish proportionally in the diet differed two–threefold between years, with the proportion of marine fish and round gobies increasing during the study period. Weights of smelt and Ruffe in the diet were larger during spring, whereas Perch, Roach and Pikeperch were higher in summer.
3. The most important foraging area for Great Cormorants from the Juodkrantė colony is Curonian Lagoon. Fish caught in the Lagoon comprised 90.6% in the cormorant diet by biomass.
4. The pellet analysis method is accurate enough for quantitative analysis of diet composition. The contribution of marine fish to Great Cormorant diet composition as calculated by applying a stable isotope mixing model, was 16.5±4.4% by weight, which confirmed the value of 17.7% estimated by pellet analysis.
5. Great Cormorant feeding on fish was size and species selective for their prey. Small fish dominated the diet, with 77.9% up to 12.5 cm length. Mean length (TL) of fish
identified in pellets was 9.4±4.2 cm and mean weight was 15.4±31.9 g. The proportions of Perch, Roach and Pikeperch in the Great Cormorant diet were greater than in the Curonian Lagoon fish community. Jacobs’ selectivity index was 0.2, 0.4 and 0.6 accordingly. Negative selectivity index values were estimated for White Bream and Ruffe, being –0.3 and –0.4 respectively.

6. Commercially targeted fish species dominated the Great Cormorant diet. These species comprised 76.9% of the total biomass consumed. Commercial size fish comprised 26.4% of total consumption, among which 26.4% (mostly Roach, 18.8%) were of commercially harvestable size. Great Cormorants and 40–45 mm mesh size commercial gillnet fishing exploit fish of different lengths, to the extent that direct competition is negligible. Great Cormorants from the Juodkrantė colony consumed 729.2±86.1 t of fish per year in 2005–2010, of which 653.3±59.4 t (14.5±1.4 kg / ha) came from Curonian Lagoon.

7. Spatial analysis fish abundance in Curonian Lagoon could not confirm the assumption that Great Cormorant predation can reduce prey fish abundance near the colony.

8. Analysis of the Curonian Lagoon fish community monitoring data from 1993–2011 showed no significant change in fish biomass. Neither total, nor the most important prey fish species biomass did not change statistically significant during the time interval, covering periods of low Great Cormorant abundance, through an exponential increase in numbers, to a stable period of high abundance.

9. Great Cormorants are effectively adapting to changes in food resources by changing their foraging strategy. Since its first detection in cormorant pellets in 2007, during the following three years the invasive Round Goby became one of the most important species in the diet and comprised 8.7% by biomass in 2010. The majority of round gobies identified in pellets, 80.6% by weight, were caught in the Baltic Sea. The importance of marine feeding increased subsequently to the gobies expansion. The proportion of marine species by biomass in the diet increased from 7.5% in 2005–2008 to 13.3% in 2009–2010. The increasing importance of gobies in the diet appears to have changed the role of Great Cormorants in the ecosystem.

Kormoranų poveikio žuvų populiacijoms vertinimui būtinas jų mitybos tyrimas, įvertinant jų raciono kokybėnę ir kiekvieną sudėtį, ilgalaikį ir sezoninį kitimą, selektyvumą, padalį žuvų rūšį ir dydį, žuvų suvartojimą. Taip pat būtini ir ichtiologiniai tyrimai, siekiant nustatyti žuvų rūšinę sudėtį, žuvų bendrijos dinamiką, žuvų populiacinius parametrus.

**Darbo tikslas** - nustatyti Juodkrantės kolonijoje perinčių kormoranų raciono sudėtį ir poveikį žuvų populiacijoms bei jų bendrijai Kuršių mariose.

**Darbo uždaviniai:**
1. Ištirti kiekvieną ir kiekvieną Juodkrantės kolonijoje perinčių kormoranų raciono sudėtį, įvertinant svarbiausias žuvų rūšis, kitimą, laiką, selektyvumą;
2. Naudojant stabiliųjų izotopų sudėties mažiosio modelį, įvertinti atrajų analizės metodo patikimumą;
3. Įvertinti vandens telkiniių svarbą kormoranų mitybai ir žuvų suvartojimą juose;
4. Įvertinti verslinių žuvų svarbą kormoranų racione, verslinės žvejybos ir kormoranų konkurenciją;
5. Remiantis erdvinio ichtiologinio tyrimo ir daugiamečio Kuršių marių žuvų bendrijos monitoringu ir erdvinio ichtiologinio tyrimo duomenimis, įvertinti kormoranų poveikį Kuršių marių žuvų populiacijoms ir jų bendrijai Kuršių mariose.
**Darbo naujumas.** Šiame darbe pirmą kartą įvertintas didžiųjų kormoranų poveikis populiacijoms tų žuvų rūšių, kuriomis daugiausia jie minta, Baltijos jūros pietų regione, kurį pastaruosius porą dešimtmečių apima viena iš pagrindinių kormoranų populiacijos ekspansijos krypčių. Šiam tyrimui buvo naudoti Kuršių marių žuvų bendrijos ir kormoranų mitybos ilgalaikių tyrimų duomenys. Pirmą kartą buvo vertinamas didžiųjų kormoranų poveikis erdviniam žuvų pasiskirstymui. Šio tyrimo rezultatai yra svarbūs tiek vertinant kormoranų poveikį žuvų populiacijoms, tiek ir suvokiant didžiųjų kormoranų kolonijų reguliavimo mechanizmus. Taip pat pirmą kartą buvo įvertintas kormoranų mitybos tyrinuose dažniausia naudojamo atrajų analizės metodo patikimumas raciono sudėties kiekvieniam vertinimui palyginant stabiliųjų izotopų sudėties maišymo modeliu ir atrajų analizės metodu gautus rezultatus.

**Mokslinė ir praktinė reikšmė.** Šio tyrimo rezultatai leidžia geriau įvertinti didžiųjų kormoranų ilgalaikių poveikį žuvų bendrijoms didelėse sudėtingose aukšto produktyvumo vandens sistemose. Šis darbas yra vienas iš nedaugelio kormoranų poveikio tyrimų, kuriame panaudoti tiek kormoranų mitybos, tiek žuvų bendrijos ilgalaikių tyrimų duomenys. Darbe buvo nustatytì svarbūs kormoranų poveikio vertinimui mitybos aspektai – raciono sudėtis ir jos kitimas laikė, mitybos selektyvumas, taip pat buvo įvertintas kiekybinio raciono sudėties tyrimo metodų patikimumas. Šio darbo rezultatai parodė ir svarbius ateities tyrimų aspektus, siekiant tiksliau įvertinti kormoranų poveikį žuvų populiacijoms. Mitybos selektyvumo parametrai leidžia įvertinti svarbiausių raciono žuvų kohortos atsaką į selektyvų kormoranų poveikį.

Praktinę vertę šiame darbe turi kormoranų ir žvejų verslininkų tiesioginės ir netiesioginės konkurencijos įvertinimas. Nors suvartojamos biomasės kiekis nebūtina įtakoja verslinių laimikų dydį, konkurencijos įvertinimas leidžia pagrįsti kormoranų populiacijos reguliavimo priemonių tikslingumą. Svarbią praktinę reikšmę gali turėti ir kormoranų poveikio invazinio juodažiočio grundo populiacijai įvertinimas.

**Ginamieji teiginiai.**
1. Atrajų analizė yra pakankamai tikslus kormoranų raciono sudėties kiekvienės tyrimo metodas;
2. Juodkrantės kolonijoje perinčių kormoranų raciono sudėtis skiriasi tiek lyginant skirtingus metus, tiek pavasario ir vasaros sezonais;
3. Kuršių marios yra svarbiausia Juodkrantės kolonijoje perinčių kormoranų maitymosis akvatorija;
4. Juodkrantės kolonijoje perinčių kormoranų mityba yra selektyvi tiek pagal žuvų rūšį, tiek pagal žuvų dydį;
5. Kormoranų poveikis nėra pakankamai stiprus, kad sukelčius žymesnių žuvų gausumo pokytį arti Juodkrantės kolonijos esančiose akvatorijose;
6. Per laikotarpių, apimantį didžiųjų kormoranų Juodkrantės kolonijos augimo ir stabilizacijos periodus, nei svarbiausių kormoranų raciono rūšių, nei bendra žuvų biomasė Kuršių mariose nekito;
7. Didieji kormoranai, keisdami mitybos strategiją, efektyviai prisitaiko prie kintančių maisto ištakų. Kuršių mariose ir Baltijos jūroje plintantis invazinis juodažiotis grundo per trumpą laiką tapo viena svarbiausių žuvų kormoranų racione.
Rezultatų pristatymas ir aprobavimas. Disertacijoje darbo tematika paskelbtos 4 mokslinės publikacijos. Darbo rezultatai pristatytų 7 tarptautinėse konferencijose.


Litaratūros apžvalga


Tyrimo vieta


Medžiaga ir metodai

pagal atskiras žuvų rūšis ir dydį, buvo laikoma, kad jauniklių maisto sudėtis nesiskyrė nuo suaugusių paukščių. Kormoranų maisto sudėtis išskirius iš kolonijos buvo vertinama kaip esančių kolonijoje vasaros laikotarpio. Kormoranų skaičius dinamika sezone eigoje ir fenologija vertinti pagal paukščių apskaitas ir daugiamečių stebėjimus (Dagys ir kt. 2004, J. Zarankaitė 2012, asm. pr.). Suvartojimo vertinimui naudotas vidutinis suaugusio kormorano dienos maisto suvartojimas 494 g (Ridgway 2010, Schmid ir kt. 1995), nustatytas respirometriiniu metodu laboratorijos sąlygomis pagal rekomenduojamus asimilacijos efektyvumo koeficientą 0,8 ir vidutinę žuvų energinę vertę 5,42 kJ·g⁻¹ (Carss ir kt. 1997). Jauniklių suvartojimo vertinimui naudotas vidutinis dienos maisto suvartojimas per visą buvimo lizde laikotarpį, nustatytas naudojant po lizdu sumontuotas svarstyklės, siekė 408 g (Carpentier ir Marion 2003).

**Ichtiologinis tyrimas.** Kormoranų ilgalaikio poveikio žuvų populiacijoms vertinimui naudoti Kuršių marių žuvų bendrijos monitoringo duomenys. Monitoringas buvo vykdomas kasmet nuo 1993 m. pagal standartinę metodiką (Thoresson 1993) dviejose akvatorijose priešais Atmatos žiotis ir ties Dreverna (1 pav.) liepos mėnesio antroje pusėje. Žuvų gausumui ir biomasei išreikšti naudojamas standartizuotas rodiklis – laimikiai pastangai – standartiniu tinklu rinkiniu per naktį vienoje sugautų žuvų skaičius arba biomase (angl. Catch Per Unit Effort, CPUE). Tvirtant kormoranų poveikį erdviniam žuvų pasiskirstymui, vykdytos mokšlinės žvejybos Kuršių marių vakariniami pakraštystėje 12-øjė skirtingu atstumu (iki 23 km) nutołių nuo kormoranų kolonijos akvatorijų (1 pav.). Tyrimas vykdytas 2009 m. (liepos mėn. 10–31 d.) ir 2010 m. (liepos mėn. 22–25 d.). Žvejybos buvo naudotas šešių skirtingos akies dydžio kaproninių žiauninių tinklainių rinkinys – 14-17,25-30-33 mm.


**Statistiniai metodai.** Statistinėje duomenų analizėje naudotas kritinis p lygmuo 0,05. Vidurkiai pateikti nurodant standartinį nuokrypį (±SD), jei nenurodyta kitaip. Raciono žuvų dydžio bei masės apskaičiavimui naudotas tiesinė, polinominė ir laipsninė regresijos. Skirtumų analizėi naudoti t testas, vienfaktorinė ANOVA, neparametriniai Mann-Whitney U ir χ² testai. Mitybos selektyvumui vertinti naudotas Jacobs
Didžiųjų kormoranų mityba. Juodkrantės kolonijoje perinčių didžiųjų kormoranų racione identifikuotos 34 žuvų rūšys bei du neidentifikuoti iki rūšies taksonai (grundalai Pomatoschistus sp. ir tobiai (Ammodoidae)) (1 lent.). 13 rūšių žuvys buvo aptinkamos kormoranų atrajose kiekvienais metais, jos sudarė 91,9 % kormoranų racione pagal masę. Svarbiausios kormoranų racione buvo karpinių (Cyprinidae) ir ešerinių (Percidae) šeimų žuvys, sudariusios atitinkamai 21 % ir 62,1 % racione pagal skaičių bei 47,3 % ir 38 % pagal mašę. Be žuvų, kormoranų atrajose buvo aptikta 4 rūšių vėžiagvyčių liekanų: smėlinės krevetės (Crangon crangon), jūrų tarakono (Saduria entomon), apželtkojo krabo (Eriocheir sinensis) ir rainuotojo vėžio (Orconectes limosus).

Trijų kormoranų racione žuvų rūšių vidutinis sutinkamumo dažnis atrajose per visą mitybos tyrimo laikotarpį buvo didesnis nei 60 %: pūgžis 80,4 %, kujojas 75,9 % ir ešeris 68,5 %, dar 5 rūšių žuvys buvo aptiktos dažniausiai nei 10 % atrajų (2 pav.). Per tyrino laikotarpį didėjo juodažiojo grando sutinkamumo atrajose dažnis. Jis vidutiniškai buvo 9,9 %, o 2009 – 2010 m. sutinkamumo dažnis siekė 21,6 %.

Analizuojant atrajas, iš viso buvo identifikuota 28180 žuvų. Identifikuotų žuvų skaičius vienoje atrajoje buvo nuo 1 iki 162, vidutiniškai 27,7 žuvys. Pagal skaičių (3 pav.) kormano racione gausiausios buvo 3 rūšių žuvys: pūgžys – 40,4 %, ešeris – 20,5 % ir kujoja – 16,9 %, jų bendra dalis racione sudarė 77,7 %. Iš likusių žuvų kiek gausesnė buvo tik stinta (Osmerus eperlanus), jos dalis racione pagal skaičių buvo 8,8 %. Kitų mitybos žuvų tarpe nei vienos rūšies dalis pagal skaičių nesiekė 4 %.

Pagal mašę (3 pav.) kormano racione didžiausiai dalį sudarė 3 rūšių žuvys: kujoja sudarė 37 %, ešeris – 16,2 %, pūgžys – 17,2 %. Bendra šių žuvų dalis racione sudarė 70,3 %. Tarp kitų mitybos žuvų rūšių sterko (Sander lucioperca) dalis pagal mašę siekė 4,6 %, kitų rūšių buvo mažesnė nei 4 %.

Juodkrantės kolonijoje perinčių kormoranų atrajose jūrinių žuvų liekanų vidutinis sutinkamumo dažnis per tyrino laikotarpį siekė 20,1 %, gėlavandenų bei diadrominių žuvų – 94 % (2 pav.). Jūrinių žuvų vidutinė dalis kormoranų racione pagal mašę siekė 9,4 %. Dviejų šaltinių maišymo modelių naudojant δ13C nustatyta jūrinių žuvų dalis kormoranų racione jauniklių maitinimo laikotarpio gugužės mėnesių ir birželio mėnesio pradžioje siekė 16,5±4,4 % (±SE). Tuo pačiu laikotarpiu pagal atrajų analize nustatyta kormoranų racione sudėtį pagal mašę jūrinių žuvų dalis siekė 17,7 %.

Per visą tyrino laikotarpį didžiojo kormorno atrajose identifikuotų žuvų vidutinis ilgis (TL) buvo 9,4±4,2 cm, vidutinė mašę 15,4±31,9 g. Juodkrantės kolonijoje perinčių kormoranų racione vyrao nedidelės žuvys, 82,8 % pagal skaičių priklausė 12 cm ir mažesnio ilgio grupėms, jų dalis racione pagal mašę sudarė 33,8 % (4 pav.). Didžiausios atrajose identifikuotos žuvys buvo 40,1 cm ilgio ir 466,3 g svorio vėgėle (Lota lota), 39,1 cm ir 101,5 g Europinis ungury (Anquilla anquilla), 37,1 cm ir 446 g sterkas, 35,1 cm ir 699,2 g lynes (Tinca tinca) (1 lent.). Dauguma žuvų, kuriomis mito kormoranai,
buvo jaunos, priklausančios mažoms ilgio grupėms. 83,1 % visų atrajose identifikuotų kuojų priklausė 4–16 cm ilgio grupėms (1–4 metų amžiaus). Sparčiau nei kuojos augančių ešerų tarpe kormoranų racione 2–10 cm ilgio grupėms priklausančios, 1–2 metų amžiaus žuvys sudarė 79,5 % visų atrajose identifikuotų ešerų. Verslinio dydžio (>18 cm, TL) trijų metų ir didesnio amžiaus ešeriai kormoranų mityboje sudarė 2,1 % raciono pagal skaičių, atitinkamai verslinio dydžio kuojos (tokio pat ilgio, 5 ir daugiau metų) sudarė 12,7 %. Verslinės žvejybos 40 ir 45 mm tinklais ir kormoranų mitybos eksploatuojamų išteklių persidengimas pagal ilgį buvo nežymus. Versliniūose laimikiuose vyravo nuo 25 cm ilgio, 8 m. ir didesnio amžiaus kuojos bei 25 cm ir didesni, 5–6 m. amžiaus ešeriai. Šiais įrankiais sugautuose ešerų laimikiuose didesnės nei 25 cm ilgio žuvys sudarė 80 %, tuo tarpu kormoranų suvartojamų ešerų tarpe – tik 0,2 % pagal skaičių, 4,7 % pagal masę. Atitinkamai tokio paties dydžio kuojos sudarė 90,8 % šiais tinklais sugautuose kuojų laimikiuose, o kormoranų racione – 2 % pagal skaičių, tačiau buvo svarbios pagal masę - sudarė 17 %.

Kuojos, ešerio ir pūgžlio skirtingų ilgio klasės dažnis 2008–2010 m. kormoranų atrajose ir mokslinių žvejybų laimikiuose daugeliu atvejų skyrėsi. Kormoranų mityba buvo teigiamai selektyvi mažesnių ilgio klasės žuvų atžvilgiu. Kormoranų atrajose dažniau nei moksliniuose laimikiuose pasitaikė 9–10 cm ilgio pūgžliai (išskyrus 2008 m., kai visų mažesnio nei 15 cm ilgio klasės dažnis buvo panašus), 10–11 ir 14–17 cm ilgio ešeriai, mažesnės nei 18 cm ilgio kuojos. Kormoranų racione ir mokslinių žvejybų Kuršių mariose laimikių žuvų rūšinė sudėtis pagal skaičių 2008–2010 m. patikimai skyrėsi (χ²=27,4, p<0,0001, df=4) (5 pav.). Kormoranų raciono svarbiausių žuvų tarpe didesniu dažniu nei mokslinių žvejybų Kuršių mariose laimikiuose pasitaikė ešeriai (išskyrus 2009 m., kai dažnis nesiskyrė), kuojos ir sterka, neigiamas selektyvumo indeksas buvo plakū (Blicca bjoerkeni) (išskyrus 2008 m., kai racione dažnis buvo nežymia didesnis) ir pūgžlių (2 lent.). Kormoranų mitybos žuvys, kurių atžvilgiu buvo įvertintas mitybos selektyvumas, racionali sudėtyje pagal skaičių tarp Kuršių mariose sugautų žuvų sudarė 91,8–96,5 %, mokslinių žvejybų laimikiuose jų bendra dalis sudarė 93,6–95,7 %.

Per visą didžiųjų kormoranų mitybos tyrimą Juodkrantės kolonijoje 2005–2010 m. raciono sudėtis žymiai kito tiek pagal skaičių, tiek pagal masę (6 pav.). Pūgžlių dalis kormoranų racione kito nuo 31,3 iki 50,5 % pagal skaičių ir nuo 8,2 iki 28 % pagal masę. Kuojų dalis racione buvo nuo 10,5 iki 25,1 % pagal skaičių ir nuo 23,2 iki 51,3 % pagal masę. Ešerų dalis kito nuo 8,7 iki 31,6 % pagal skaičių ir nuo 10,2 iki 21,6 % pagal masę. Šių svarbiausių kormoranų raciono žuvų bendra dalis vyravo per visą tyrimo laikotarpį ir vyravo nuo 65,7 iki 86,5 % pagal skaičių ir nuo 61,2 iki 81,1 % pagal masę. Jūrinių žuvų dalis kormoranų racione skyrėsi apie 4 kartus, pagal skaičių jų buvo nuo 3 iki 11,9 %, pagal masę – nuo 3,2 iki 14,3 %. Per tyrimo laikotarpį išsiskyrė 2009–2010 m. periodas, kai jūrinių žuvų dalis kormoranų racione viršijo vidurkį ir siekė 14,3 % pagal skaičių bei 12,3 % pagal masę. Jūrinių žuvų pasitaikymo atrajose dažnis skyrėsi apie du kartus – nuo 13,3 iki 26,8 %. Kormoranų raciono sudėtis pavasario ir vasaros sezonais patikimai skyrėsi tiek pagal skaičių (χ²=31,7, df=4, p<0,0001), tiek pagal masę (χ²=12,1, p=0,0164, df=4) per visą tyrimo periodą 2005–2010 m., išskyrus sudėtį pagal masę 2005 m. (χ²=4, p=0,4, df=4) (7 pav.).

**Didžiųjų kormoranų suvartota žuvų masė.** Didžiųjų kormoranų perinčių porų skaičius Juodkrantės kolonijoje mitybos tyrimo laikotarpui 2005–2010 m. svyravo nuo
2362 iki 3367. Vienos kormoranų poros suvartotų žuvų masė (kartu su išaugintais jaunikliais) siekė 247,1 kg. Juodkrantės kolonijoje perinčių kormoranų bendra suvartota žuvų masė 2005-2010 m. siekė nuo 583,7 t iki 824,4 t (vidutiniškai 729,2±86,1 t), tarp jų Kuršių mariose buvo suvartota nuo 568,3 t iki 728,6 t (vidutiniškai 653,3±59,4 t). Tarp svarbiausių žuvų rūšių daugiausia suvartoto kuoju (vidutiniškai 270,7 t per metus), pūgžlių (121,8 t), ešerių (117,8 t), šių rūšių bendra suvartota masė siekė 510,2 t, 77,8 % visos suvartotos žuvų masės. Iš kitų žuvų rūšių didesni suvartoti kiekiai buvo sterkų (36,1 t), upinių plekšnių (Platichthys flesus) (26,9 t) plakių (25,7 t) ir karšių (Abramis brama) (20,6 t). Tai pat daug buvo suvartota juodąžiūčių gruadalų; laikotarpui nuo pirmo aptikimo kormoranų mityboje 2007 m. vidutiniškai suvartojimas siekė 36 t per metus. Likusių rūšių per metus suvartota vidutinė masė nesiekė 20 t. Verslinės žuvų rūšys vidutiniškai sudarė 76,9 % (561,9 t) visos suvartotų žuvų masės, verslinio dydžio žuvų buvo 26,7 %, daugiausia kuojo (18,8 %) ir ešerių (4,3 %), taip pat stintų (2,4 %). Didžiąją dalį suvartotų verslinių žuvų (88,4 %) sudarė mažos rinkos vertės (vidutinė didmeninė rinkos vertė iki 3,5 Lt/kg šviežos žuvies) žuvys (8 pav.), daugiausia kuojos, ešerių ir plakių. Didelės vertės verslinių žuvų (europinis ungurys, šlakis (Salmo trutta)) kormoranų racione identifikuotos buvo vos kelios žuvys, jų suvartotos masės dalis buvo mažesnė nei 0,05 %. Vidutinės ir didelės vertės žuvų kormoranai per metus vidutiniškai suvartodavo 63 t, daugiausia sterku ir stintų. Juodkrantės kolonijoje perinčių kormoranų suvartotų žuvų vidutinė biomasė Kuršių marių viename hektare 2005–2010 m. siekė 15,8±1,4 kg. Pagal verslinės žvėjybos laimikų statistiką tuo pačiu laikotarpiu verslinių laimikiai Lietuvai priklausančioje Kuršių marių dalyje siekė 26,9 kg/ha (3 lent.). Palyginus su verslinės žvėjybos laimikiais Kuršių mariose, kormoranai suvartoto daugiau ešerių (atitinkamai kormoranų suvartojimas 117,8 t, verslinių laimikiai 47,7 t), santykinai dideli suvartoti kiekiai buvo plakių (25,7 t ir 29,6 t) ir kuojoj (270,7 t ir 366,5 t). Kitų verslinių žuvų kormoranų suvartoti kiekiai buvo žymiai mažesni nei verslinių laimikiai. Kormoranų vidutiniškai suvartota žuvų biomasė sudarė 7,1 % visos žuvų biomasės Lietuvai priklausančioje Kuršių marių dalyje pagal 2008–2010 m. vertinimą (Repečka 2009, 2010). Pūgžlių suvartotos biomasės dalis didžiausia buvo ir siekė 24,9 % visos jų biomasės. Vidurki taip pat viršijo ešerių ir kuojų suvartojimas ir siekė atitinkamai 11,8 ir 9,1 % (3 lent.).

Didžiąjų kormoranų poveikis erdviniam žuvų pasiskirstymui. Vykdant kormoranų poveikio erdviniam žuvų pasiskirstymui tyrimą 12-oje akvatorijoje, žuvų moksliniai laimikiai 2009 ir 2010 m. nesiskyrė statistiškai patikimai nei pagal žuvų gausumą, nei pagal sugavimus pastangų (t testas; t=0,90, p=0,38 pagal gausumą, t=0,48, p=0,64 pagal biomasę; d.f.=22). Didžiąją mokslinių laimikų dalį sudarė 3 rūšių žuvys – pūgžlys, kuoją ir ešerys, jų bendra dalis pagal gausumą buvo 84,6 % (58,6–96,7 %) ir pagal masę 73,5 % (43,5–95,6 %) 2009 m. ir atitinkamai 88,4 % (63,5–98,5 %) bei 70,1 % (38–89,1 %) 2010 m. Tyrimo laikotarpiu žymiai kito kuojų ir pūgžlių dalis moksliniuose laimikiuose: kuojų laimikiai sumažėjo (27,1 % ir 10,7 % pagal skaičių, 33,4 % ir 16,8 % pagal masę), pūgžlių padidėjo (41,1 % ir 66,8 % pagal skaičių, 14,8 % ir 29,1 % pagal masę). Ešerų dalis kito mažiau (16,3 % ir 10,8 % pagal skaičių, 25,4 % ir 24,1 % pagal masę).

Tyrimo metu tiek 2009, tiek 2010 m. buvo stebėti dideli skirtumai tarp atskirų mokslinių žvejybų akvatorijų tiek pagal bendrą žuvų gausumą, tiek pagal biomasę. Dar didesni skirtumai (iki kelių dešimčių kartų) tarp akvatorijų buvo pagal svarbiausių
bendrijos žuvų, kuojos, pūžlio ir ešerio santykinių gausumą. Palyginus moksliinių žvejybų sugavimus tarp skirtingų akvatorijų, abejus tyrimo metus statistiškai patikimi skyrėsi tiek bendras žuvų gausumas, tiek svarbiausių žuvų rūsių gausumas ir sugavimai pastangai. Visų žuvų sugavimai pastangai skirtingais metais tose pačiose akvatorijose nesiskyrė ($\chi^2$ testas; $\chi^2=16,43$, $p=0,126$, df=11).

Standartizuotas visų žuvų gausumas (CPUE) neigiamai koreliavo su atstumu nuo Juodkrantės kormoranų kolonijos (4 lent.). Neigiamas ryšio pobūdis išliko abejus tyrimo metus, bet 2009 m. buvo stipresnis (Spearman’o koreliacija, $r=-0,73$). 2009 m. su atstumu nuo kolonijos neigiamai koreliavo ir sugavimai pastangai, taip pat ir pūžlio, ešerio bei kuojos gausumas ir sugavimai pastangai. 2010 m. bendro žuvų gausumo ir sugavimų pastangai ryšys su atstumu nuo kolonijos buvo silpnas, pūžlio išliko neigiamai koreliacija kaip ir 2009 m. Ešerio gausumo ir sugavimų ryšio su atstumu nuo kolonijos pobūdis 2010 pakito ir koreliavo teigiamai (atitinkamai $r=0,52$ bei $r=0,22$). Panašiai, tačiau silpniau, pakito kuojų kojuo gausumas ir biomasė. (9 pav.)

Ilgalaikis kormoranų poveikis žuvų populiacijoms ir jų bendrijai Kuršių mariose. Per visą žuvų bendrijos Kuršių mariose monitoringo laikotarpį 1993–2011 m. žuvų biomasė ir gausumas moksliiniuose laimikiuose nepakito (tiesinė regresija; biomasė: $r^2=-0,05$, $F=0,17$, $p=0,68$; gausumas: $r^2=-0,05$, $F=0,13$, $p=0,73$), tačiau buvo žymūs svyravimai (10 pav.). Biomasė (CPUE) per šį laikotarpį skirtingais metais skyrės daugiau nei 3 kartus ir varijavo nuo 18,1 kg iki 52,2 kg. Tiek žuvų biomasė, tiek gausumas monitoringo Atmatos akvatorijoje buvo didesni nei Drevernos ir skyrės statistiškai patikimai (ANOVA; biomasė: $F_{2,38}=573,4$, $p<0,01$, gausumas: $F_{2,38}=618,3$, $p<0,01$). Atmatos akvatorijoje žuvų biomasė ir gausumas žvejybos pastangai buvo atitinkamai 35,6±17,7 kg ir 478±230 vnt., Drevernos akvatorijoje atitinkamai siekė 25,9±12,9 kg ir 394±230 vnt. Abiejose monitoringo akvatorijose kuojos, ešerio ir pūžlių sudarė didžiąją biomasės dalį laimikiuose, ties Atmata šių rūsių dalis buvo 65,6±17,4 %, ties Dreverna – 77,1±13,1 %. Bendra žuvų biomasė ir gausumas Atmatos ir Drevernos akvatorijose taip pat nekito (tiesinė regresija; $p>0,5$). Taip pat nekito ir svarbiausių žuvų rūsių biomasė, išskyrus kuojų biomasę ties Atmata – ji didėjo, tačiau nežymiai (tiesinė regresija; $r^2=0,04$, $F=7,17$, $p<0,01$). Kormoranų skaičiaus ir žuvų biomasės ir gausumo ryšys buvo silpnas ir statistiškai nereikšmingas abejose monitoringo akvatorijose (tiesinė regresija; $p>0,47$). Bendros ir kormoranų raciono svarbiausių žuvų biomasės kitimo Kuršių marių monitoringo laimikiuose 1993–2010 m. ir ryšio su kormoranų gausumu bei verslinės žvejybos poveikiai perteklinės analizės (RDA) rezultatai parodė, kad ne kormoranų skaičius, nei verslinės žvejybos intensyvumas neturėjo žymesnio poveikio (11 pav.). Kartu šie veiksmai paaškinėjo 17 % žuvų biomasės kitimo monitoringo laimikiuose ($p=0,001$).

Perinčių kormoranų porų skaičius Juodkrantės kolonijoje nuo 1993 iki 2011 m. išaugo nuo 195 iki 3808. Kormoranų suvartojamų žuvų biomasė Kuršių mariose didėjo nuo 45 t 1993 m. iki 729 t 2010 m. Kormoranų suvartojamos žuvies kiekis kito panašiai kaip ir verslinės žvejybos laimikiai (išskyrus 2009–2010 m.) ir padidėjo per tą patį laikotarpį daugiau kaip 600 t. Tuo pačiu laikotarpiu verslinės žvejybos laimikiai šiuo
Invazinis juodažiotis grūdalis didžiųjų kormoranų mityboje. 2007–2010 m. tiriant invazinio juodažiočio grūdalo gausumą Kuršių mariose, buvo stebimas laipsniškas jų plitimas bei gausumo didėjimas pietų kryptimi nuo Klaipėdos uosto. 2007 m. juodažiočiai grūdai buvo pagauti ties Juodkrante, 2010 m. buvo brandinių laimikiuose ties Vente. Akvatorijos su didesniu grūdalo gausumu (daugiau nei 10 individų 1000 m²) taip pat buvo registruojamos vis toliau pietų kryptimi – 2007 m. ties Alksnyne, 2010 m. ties Avikalnio ragu. Didžiasias gausumas buvo stebėtas 2009 m. ties Lybio ragu (75 individai, 0,6 kg 1000 m²) ir ties Juodkrantės kormoranų kolonija (251 individas, 0,8 kg 1000 m²), šiuose taškuose juodažiočiai grūdai sudarė atitinkamai 51,3 % ir 46,8 % visos žuvų biomasės jaunikliniame brandinyje.

Didžiojo kormorano racione juodažiočio grūdalo pirmą kartą buvo identifikuotas 2007 m. ir sudarė 0,6 % mitybos pagal skaičių bei 0,3 % pagal masę. Vėliau jų svarba racione didėjo ir 2010 m. juodažiočio grūdalo sudarė 8,7 % kormoranų raciono sudėties pagal svorį, o bendra Juodkrantės kolonijos kormoranų suvartojama biomasė per metus siekė 70,6 t (12 pav.). Juodažiočio grūdalo svarba kormoranų racione kito priklausomai nuo sezono, didesnė dalį pagal masę sudarė pavasarį, 2009 m. atitinkamai pavasarį ir vasarą buvo 9 % ir 6 %, 2010 m. 12,2 % ir 7 %. Didžioji dalis pagal masę (73,4–90 %) kormoranų atrajose identifikuotų grūdų buvo pagauti Baltijos jūroje. Gausėjant grūdalams, kito mitybos Baltijos jūroje svarba. 2005–2008 jūrinės žuvys kormoranų racione pagal masę vidutiniškai sudarė 7,5 %, 2009–2010 m. kartu su jūroje sugautais juodažiočiais grūdais – 13,3 %.

Rezultatų aptarimas


Didžiųjų kormoranų Juodkrantės kolonija yra įsitikinusi greta Baltijos jūros ir Kuršių marių, vandenų, pasižymėjusi didelė žuvų įvairovę (1 pav.). Šio ilgalaikio, 2005–2010 m. vykusio tyrimo metu kormoranų mityboje buvo identifikuota dauguma irpastomių laikomų žuvų rūšių (Repečka 2003a) (1 lent.). Per visą tyrimo laikotarpį kormoranų


Juodkrantės kolonijoje perinčių kormoranų mitybos tyrimo nustatytų žymūs maisto sudetės sezoniniai skirtumai, svarbiausių žuvų dalis pavasarį ir vasarą skyreši daugiau nei 2 kartus (stintų daugiau nei 15 kartų). Dėl to ir dėl kormoranų gausumo dinamikos metų eigoje poveikio stiprumas atšikoems mitybos žuvų rūšims kito. Be to, nuo vasaros vidurio kormoranų maisto sudėtyje nemažą dalį sudaro paaugę žuvų jaunikliai, pavyzdžiui, 2010 m. liepos mėn. pabaigoje – rugpjūčio mėn.pradžioje net 80 % visų atrajose identifikuotų ešerių buvo mažesni nei 6 cm ilgio šiumetukai.


Dar vienas kormoranų poveikio aspektas – mityba saugomomis žuvės rūšimis. Kormoranai didžiaja dalimi yra plėšrūnai apsakotiniai, todėl paprastai retos žuvų rūšys sudaro nedidelę jų racino dalį. Bendrijos svarbos žuvų rūšių, įtrauktų į Buveinių direktyvos II priedą, 3 buvo identifikuotos kormoranų atrajose – perpelė (Alosa fallax), salatis (Aspius aspius) ir ožka (Pelecus cultratus). Šios žuvys sudarė labai nedidelę racino dalį, suvartota jų biomasė sudarė 1,3 % racino.


Išvados

1. Juodkrantės kolonijoje perinčių didžiųjų kormoranų racionui būdinga didelė rūšinė įvairovė. Buvo identifikuotos 34 žuvų rūšys ir du iki rūšies neidentifikuoti taksonai. Svarbiausios racione pagal masę buvo 3 rūšių žuvys – kuojų (37 %), pūgžlysu (17,2 %) ir ešerys (16,2 %), jų bendra dalis buvo 70,3 %.


4. Atrajų analizės metodas yra tinkamas metodas kiekvienam raciono sudėties tyrimui. Stabilūų izotopų sudėties maišymo modeliui nustatyta kormoranų raciono kiekvienė sudėtis patvirtino atrajų analizės rezultatus, to paties laikotarpio jūrinių žuvų dalis mityboje atitinkamai buvo 16,5±4,4 % ir 17,7 %.

5. Kormoranų mityba buvo selektyvi tiek pagal žuvų dydį, tiek pagal rūšį. Racione vyra vo smulkius žuvys, 77,9 % jų buvo mažesnės nei 12,5 cm ilgio. Vidutinis atrajose identifikuotų žuvų ilgis (TL) buvo 9,4±4,2 cm, vidutinė masė 15,4±31,9 g. Ešeriu, kuojų ir sterkų atrajose buvo aptinkami dažniau nei Kuršių mariose, Jacobs selektyvumo indeksas atitinkamai buvo 0,2, 0,4 ir 0,6. Plakiams ir pūgžliams nustatytas neigiamas selektyvumo indeksas, atitinkamai –0,3 ir –0,4.
6. Kormoranų racione vyravo verslinės žuvų rūsys. Jos sudarė 76,9% visos suvartotų žuvų biomasės, 26,4% žuvų buvo verslinio dydžio, daugiausia kuojos (18,8%). Kormoranai ir verslinė žvejyba Kuršių mariose (40–45 mm tinklais) eksplotuoja skirtingo dydžio žuvis, tiesioginė konkurencija yra nežymė. Bendra Juodkrantės kolonijoje perinčių kormoranų suvartotų žuvų biomasė per metus (2005–2010) siekė 729,2±86,1 t, iš jų 653,3±59,4 t (14,5±1,4 kg/ha) Kuršių mariose.

7. Erdvinis žuvų gausumo tyrimas Kuršių mariose nepatvirtino prielaidos, kad dėl kormoranų poveikio arti kolonijos esančiose akvatorijose gali sumažėti žuvų gausumas.


9. Didieji kormoranai efektyviai prisitaiko prie kintančių maisto išteklių. 2007 m. pirmą kartą kormoranų atrajose aptiktas invazinis juodažio grasukas, per sekančius trejus metus tapo viena svarbiausių žuvų rūšių racione ir 2010 m. sudarė 8,7% pagal masę. 80,6% pagal masę kormoranų atrajose identifikuotų juodažiočių grunštalų buvo sugauti Baltijos jūroje, todėl, jiems gausėiant, didėjo mitybos Baltijos jūroje svarba: nuo 7,5% 2005–2008 m. iki 13,3% 2009–2010 m. Grunštalų svarbos racione didėjimas keičia kormoranų vaidmenį ekosistemoje.

Scientific approval
Mokslinis pagrindimas

List of publications:
Publikačijos:
Presentations in international conferences:
Pranešimai tarptautinėse konferencijose:
Curriculum vitae

Name: Žilvinas Pūtys

Date and place of birth: 13 February, 1971, Plungė district, Lithuania

Education: 2007-2011 PhD studies at the Institute of Ecology of Vilnius University
1989-1995: Master Degree in Biology, Faculty of Natural Sciences, Vilnius University;

Professional experience: 2006-2009 research assistant, Institute of Ecology of Vilnius University
2010-present research assistant, Nature Research Centre, Institute of Ecology

Contacts: Nature Research Centre, Institute of Ecology, Laboratory of Marine Ecology, Akademijos st. 2, LT-08412, Vilnius, Lithuania