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## **Ecological commonalities among pelagic fishes: comparison of freshwater ciscoes and marine herring and sprat** — [Source link](#)

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3 **of freshwater ciscoes and marine herring and sprat**

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5 **Ingeborg Palm Helland · Franz Hölker ·**  
6 **Jan Ohlberger · Myron A. Peck**

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14 ecological interactions, behavioural ecology and physio-  
15 logical ecology of temperate and Arctic freshwater core-  
16 gonids (vendace and ciscoes, *Coregonus* spp.) and marine  
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19 warming on these groups of fish based on the ecological

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36

**Introduction** 37

Fishes are the most diverse group of vertebrates, and 38  
almost all aquatic systems (apart from ground-water) sup- 39  
port their populations. They have developed an astonishing 40  
variety of life styles, feeding modes, morphological adap- 41  
tations and physiological specializations. However, a major 42  
distinction seems to exist between fishes living in fresh- 43  
water and those living in marine environments. This dis- 44  
tinction is less a biological reality and more a difference 45  
in the traditional conceptualisation by the researchers who 46  
work within these two different aquatic habitats. This 47  
division has likely arisen and continues to be supported by 48  
the physical separation of working groups between marine 49  
and freshwater research institutes, which prevents contin- 50  
ued exchange of ideas and fruitful collaborations across 51  
aquatic borders. Our contribution aims to bridge this 52

53 division by explicitly comparing groups of fish residing in  
54 either of these two main aquatic habitats to find com-  
55 monalities and fundamental differences. By merging teams  
56 of freshwater and marine researchers, the aim of this syn-  
57 thetic work is to identify research gaps and future topics  
58 common across aquatic habitats.

59 We focus on dominant pelagic planktivores, the core-  
60 gonids in freshwater lakes and the clupeids in marine and  
61 brackish waters. Both groups of fish are of high importance  
62 to commercial and recreational fisheries (Nyberg et al.  
63 2001; Stockwell et al. 2009; Geffen 2009; Dickey-Collas  
64 et al. 2010). We refer in particular to the temperate, boreal  
65 and Arctic zones, with a comparison between freshwater  
66 ciscoes (*Coregonus* spp.) living in lakes, and the Baltic and  
67 North Sea herring (*Clupea harengus*) and sprat (*Sprattus*  
68 *sprattus*). We give more examples for the species of the  
69 European temperate zone, because the authors' long  
70 research history on these groups facilitates a detailed  
71 understanding of the ecology and evolution of these fishes.  
72 We explicitly add reference and comparison to Siberian  
73 and North-American coregonids for some patterns or pro-  
74 cesses, but do not cover the species from these geograph-  
75 ical areas with similar detail. The emerging reason for our  
76 comparison, to be demonstrated by this review, is a sur-  
77 prisingly high number of biological features that are shared  
78 by coregonids and clupeids, not least a similar morphology  
79 and coloration (Fig. 1). We start by reviewing results on  
80 evolutionary history and population genetics to elucidate  
81 the local variability of the focal fish groups. We continue  
82 reviewing reproduction and life history, ecological inter-  
83 actions, behavioural ecology and physiological ecology.  
84 Finally, we elucidate potential effects of climate change on  
85 both groups of fish, thus mirroring the general theme of the  
86 AQUASHIFT priority program (see this Special Issue of  
87 Marine Biology for more examples). Generally, we start by  
88 discussing aspects of the biology of coregonids and then  
89 report on similar aspects of clupeids. We close each part by  
90 a summary, in which we explicitly compare the two groups  
91 and suggest future research topics.

## 92 Evolutionary history and population genetics

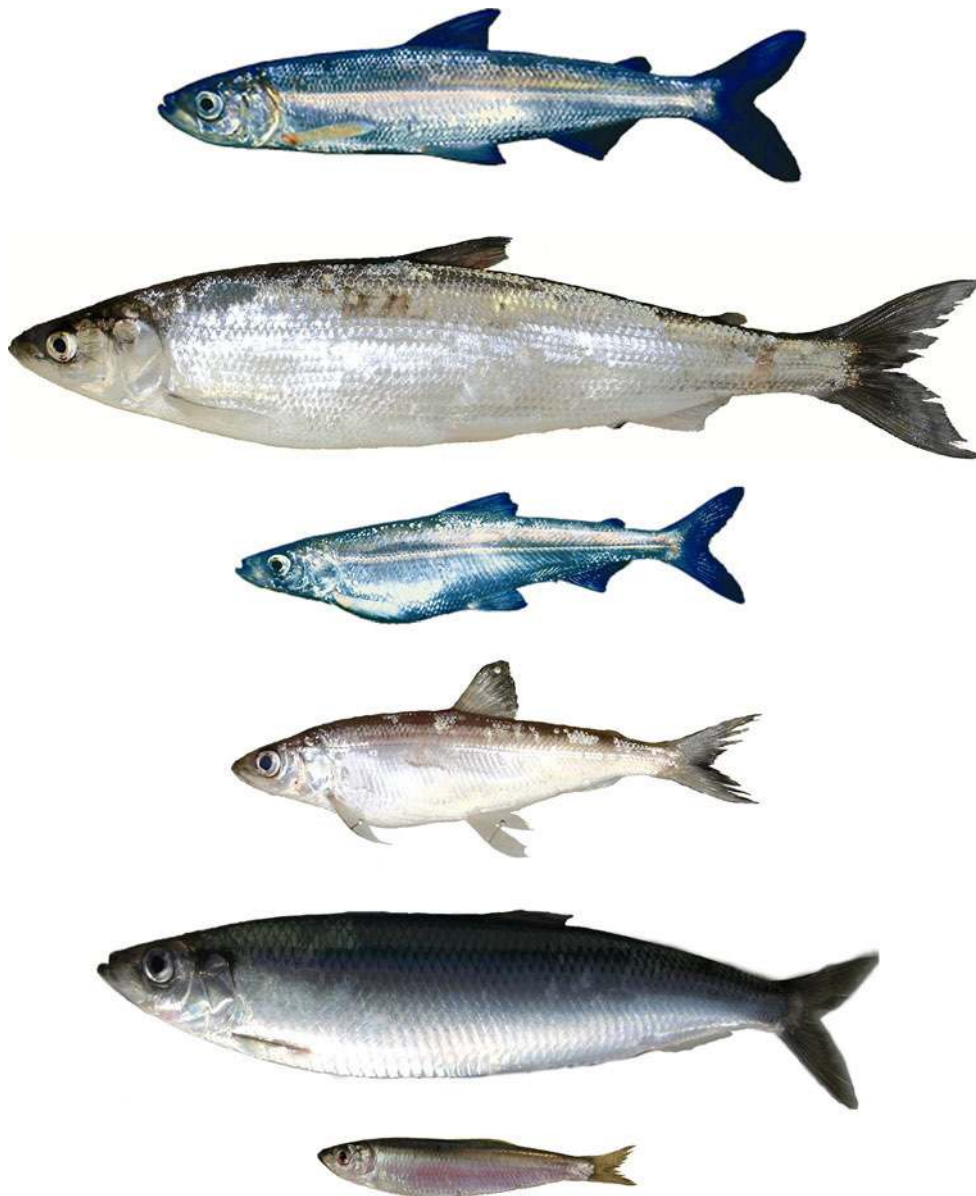
93 In the European temperate and boreal zones, only a few  
94 species of pelagic planktivorous coregonids can be found.  
95 Especially in deep lakes with a low number of other  
96 competing fish species, coregonid populations are known  
97 to segregate in their niches, mainly by specializations to  
98 either littoral, pelagic or profundal habitats. Ecological  
99 segregation is often observed for populations of whitefish  
100 (*Coregonus lavaretus*) (Østbye et al. 2005; Kottelat and  
101 Freyhof 2007; Hudson et al. 2011; Kahilainen et al. 2011b).  
102 Typically, a smaller planktivorous form residing in the

103 pelagic area lives sympatrically with one or two larger  
104 benthivorous forms found in littoral or profundal zones  
105 (Siwertsson et al. 2010). However, because usually only  
106 one morph is strictly pelagic, we do not consider popula-  
107 tions of *C. lavaretus* in more detail here.

108 The other widely distributed European pelagic *Coreg-*  
109 *onus* species is vendace (*Coregonus albula*) (Fig. 1) that is  
110 common in deep, oligo- to mesotrophic lakes of Scandi-  
111 navia and northern Germany, Poland and Russia (Kottelat  
112 and Freyhof 2007; Mehner et al. 2007a). Vendace spawn in  
113 late autumn in most of the lakes. In a few lakes of Scan-  
114 dinavia, Russia and Germany, spring-spawning ciscoes are  
115 found, primarily sympatric with vendace. Lake-endemic  
116 spring-spawning species with viable populations are  
117 *C. lucinensis* (Fig. 1) from Lake Breiter Luzin (Germany)  
118 (Thienemann 1933), *C. fontanae* from Lake Stechlin  
119 (Germany) (Schulz and Freyhof 2003), *C. trybomi* from  
120 Lake Fegen (Sweden) (Svårdson 1979) and *C. kiletz* and  
121 *C. ladogae* from Lakes Onega and Ladoga (Russia),  
122 respectively (Pravdin 1936). Similar spring-spawning spe-  
123 cies usually referred to as *C. trybomi* have existed or still  
124 exist in some lakes of Finland and Karelia (Airaksinen  
125 1968) and may have gone extinct in three other Swedish  
126 lakes (Kottelat and Freyhof 2007).

127 Studies on genetic differentiation between these popu-  
128 lations of sympatric and allopatric ciscoes are rare. By  
129 studying enzyme gene variability of Finnish populations,  
130 Vuorinen et al. (1981) concluded that autumn-, winter- and  
131 spring-spawning populations do not form monophyletic  
132 units. More detailed genetic analyses by using a range of  
133 marker sets revealed a complex phylogeographical history  
134 of the German sympatric populations (Schulz et al. 2006;  
135 Mehner et al. 2010b). Spring-spawning ciscoes were  
136 genetically most closely related, but formed a separate  
137 cluster together with their sympatric vendace populations  
138 relative to other allopatric vendace populations. This pat-  
139 tern suggests the potential of parallel sympatric speciation  
140 in both lakes, but the genetic signature modified by sec-  
141 ondary contacts and partial hybridization with other  
142 *Coregonus* lineages (Mehner et al. 2010b). Furthermore,  
143 there was a significant isolation-by-distance pattern in the  
144 genetic differentiation between German vendace popula-  
145 tions (Mehner et al. 2009). Therefore, partial isolation and  
146 local adaptation in the often small lakes contribute to the  
147 evolutionary history of *Coregonus* populations despite the  
148 relatively short time since last glaciation.

149 Well-defined cisco species from Siberia and Northwest  
150 America encompass least cisco (*Coregonus sardinella*),  
151 Bering cisco (*C. laurettae*) and Arctic cisco (*C. autumnalis*)  
152 (Turgeon and Bernatchez 2003; Politov et al. 2004), the  
153 latter also occurring in Ireland (Harrod et al. 2001).  
154 Only *C. sardinella* are primarily living in lakes, whereas  
155 *C. laurettae* and *C. autumnalis* are anadromous (Brown et al.



**Fig. 1** Photographs of a number of coregonids and clupeids discussed in this paper. From *top to bottom* *Coregonus albula* (Lake Breiter Luzin, 120 mm total length (TL), picture: Jörg Freyhof); *Coregonus artedi* (Lake Superior, 386 mm TL, picture: Gary Cholwek); *Coregonus lucinensis* (Lake Breiter Luzin, 122 mm TL,

picture: Jörg Freyhof); *Coregonus hoyi* (Lake Superior, 212 mm TL, picture: Zach Woiak); *Clupea harengus* (Western Baltic, 285 mm TL, picture: Sophie Bodenstern); *Sprattus sprattus* (Bornholm basin of Baltic Sea, 123 mm, picture: Holger Haslob)

156 2007), and *C. atumnalis* phenotypically resemble more the  
 157 European whitefishes than ciscoes (Kottelat and Freyhof  
 158 2007). A centre of coregonid diversity in North America are  
 159 the Laurentian Great Lakes, with eight species recognized  
 160 (Scott and Crossman 1973; Todd and Smith 1992) from  
 161 which longjaw cisco (*C. alpenae*) and deepwater cisco  
 162 (*C. johannae*) have gone extinct. Four of the other six species  
 163 (*C. zenithicus*, *C. reighardi*, *C. kiyi*, *C. nigripinnis*) are  
 164 threatened or vulnerable, whereas only bloater (*C. hoyi*) and  
 165 lake herring (*C. artedi*) (Fig. 1) occur in abundant popula-  
 166 tions. Recent analyses by mitochondrial and microsatellites

167 markers elucidated that genetic variation between the cisco  
 168 populations in the Great Lakes reflected geography rather  
 169 than taxonomy, and hence, it was recommended that a single  
 170 taxon (*C. artedi sensu lato*) be recognized, covering all cisco  
 171 species in the Great Lakes (Reed et al. 1998; Turgeon et al.  
 172 1999; Turgeon and Bernatchez 2003). In the Great  
 173 Slave Lake (NT, Canada), *C. artedi*, *C. zenithicus* and  
 174 *C. sardinella* coexist (Vecsei et al. 2011).

175 The mechanisms and strength of genetic differentiation  
 176 between populations differ between freshwater and  
 177 marine fishes because marine environments present fewer



178 geographical barriers to dispersal and higher levels of  
179 connectivity. Accordingly, effective population sizes are  
180 large resulting in limited genetic drift, and hence, low  
181 levels of genetic population structure are common among  
182 marine fish species (DeWoody and Avise 2000; Puebla  
183 2009). Surprisingly, few studies exist on cases of ecolog-  
184 ical divergence and sympatric speciation in marine  
185 fishes similar to those often observed in the more iso-  
186 lated freshwater systems (Puebla 2009), although  
187 local adaptation and limited dispersal cannot be excluded  
188 to be important also in marine systems (Jørgensen et al.  
189 2008).

190 The Atlantic herring (*Clupea harengus*) (Fig. 1) might  
191 be a good example. This species exhibits a complex pop-  
192 ulation structure with several divergent populations refer-  
193 red to as subspecies, stocks or groups (Iles and Sinclair  
194 1982; McQuinn 1997a). Significant, albeit weak, genetic  
195 differentiation has been found between local stocks  
196 (Larsson et al. 2010), but the greatest differences were  
197 detected between the highly saline North Sea and the  
198 brackish Baltic Sea subpopulations (Bekkevold et al. 2005;  
199 Ruzzante et al. 2006; Larsson et al. 2007). A striking  
200 similarity to coregonids is the variation of spawning times  
201 of herring populations, with spawning peaks in spring,  
202 autumn and winter all occurring in the Atlantic and the  
203 adjacent North and Baltic Seas. In the Western Baltic,  
204 spring- and winter spawning, populations of herring locally  
205 coexist (Bekkevold et al. 2007). The herring stocks from  
206 the Northwest Atlantic can be divided into northern and  
207 southern groups and have different spawning times. The  
208 northern group is found from the Gulf of St Lawrence to  
209 the south coast of Greenland and spawns in spring. The  
210 southern population occupies the area south of the Gulf of  
211 St Lawrence to the Virginia coast and spawns in autumn  
212 (Klinkhardt 1996; Stephenson et al. 2009).

213 Genetic analyses by microsatellites revealed two dif-  
214 ferent processes by which winter spawning may have  
215 arisen from the otherwise dominant spring-spawning mode.  
216 In one population from inner Danish waters, a founder  
217 effect from a distant winter-spawning population was  
218 likely. In contrast, 'spawning time switching' (McQuinn  
219 1997b) from spring to winter spawning has been suggested  
220 for the herring population close to the island of Rügen  
221 (Germany), as suggested by low differentiation between  
222 spring- and winter spawners (Bekkevold et al. 2007).

223 No genetic differences between spawning populations  
224 have been found for sprat (*Sprattus sprattus*) (Fig. 1), the  
225 other common pelagic clupeid in European temperate  
226 marine ecosystems (Limborg et al. 2009). This is in part  
227 surprising because sprat show distinctly separate spawning  
228 grounds in the Baltic Sea (Arkona, Bornholm and Gotland  
229 basins) as well as seasonally changing circulation patterns,  
230 which could provide regionally self-sustaining populations.

231 Similarly, no significant genetic differentiation exists  
232 between North Sea and Baltic Sea populations of sprat  
233 (Debes et al. 2008). In contrast, strong genetic differentia-  
234 tion exists between Atlantic and Mediterranean or Black  
235 Sea stocks, coinciding with different temperature prefer-  
236 ences of the respective populations with subspecies rec-  
237 ognized (Debes et al. 2008).

## 238 Summary and comparison

239 Evolutionary significant units can be found in both core-  
240 gonids and clupeids of the temperate and Arctic zones that  
241 are considered valid species in European, Siberian and  
242 Northwest American coregonids (Turgeon and Bernatchez  
243 2003; Kottelat and Freyhof 2007), discrete phenotypes of  
244 one lineage (*C. artedi*) as the result of incipient processes of  
245 parallel diversification in the Great Lakes (Turgeon and  
246 Bernatchez 2003), and subspecies or stocks in clupeids  
247 (McQuinn 1997a). Among the coregonids, genetic differ-  
248 entiation is primarily driven by geographical distance. If  
249 different lineages came into secondary contact after last  
250 glaciation, introgression and hybridization promoted adap-  
251 tive radiations along ecological gradients (Turgeon and  
252 Bernatchez 2003; Mehner et al. 2010b). If combined with  
253 allochrony of spawning times, populations in geographi-  
254 cally isolated lakes split into discrete species (*C. fontanae* of  
255 Lake Stechlin, *C. lucinensis* of Lake Breiter Luzin) (Mehner  
256 et al. 2010b). In contrast, genetic differentiation remained  
257 weak in less-isolated systems where the populations still  
258 show overlapping spawning times (*C. artedi sensu lato* of  
259 the Great Lakes).

260 The situation is less clear for clupeids where the popu-  
261 lations show only weak genetic differentiation, and where  
262 genetic exchange between the stocks is likely due to dis-  
263 persal and straying into various reproductive areas from  
264 populations that coexist at feeding grounds (McQuinn  
265 1997a; Gaggiotti et al. 2009). Therefore, the Atlantic  
266 herring stocks are considered to form a meta-population  
267 (McQuinn 1997a). Furthermore, there is no clear corre-  
268 spondence between spawning time and genetical identity,  
269 because both 'spawning-time switching' within popula-  
270 tions and founder effects from extant populations have  
271 been shown to form local populations with deviating  
272 spawning times (Bekkevold et al. 2007). Only the latter  
273 process may produce genetical distinctness between  
274 spring- and autumn spawners and hence can be assumed to  
275 facilitate local adaptive ecological divergence similar to  
276 the processes known for coexisting spring- and autumn-  
277 spawning coregonids.

278 Overall, the pelagic fish species covered in this review  
279 mirror the gradient of ecological speciation typically found  
280 in fishes (Hendry 2009). Systems vary from continuous  
281 adaptive variation without reproductive isolation in the

282 clupeids, over discontinuous adaptive variation with minor  
 283 reproductive isolation in the Great Lakes ciscoes, to  
 284 adaptive differences with reversible reproductive isolation  
 285 in the sympatric European ciscoes and the allopatric  
 286 Siberian and Northwest American ciscoes. Recent evidence  
 287 for hybrids between vendace and European whitefish  
 288 (Kahilainen et al. 2011a) supports that irreversible repro-  
 289 ductive isolation has not yet been achieved in these post-  
 290 glacial diversifications of species.

## 291 **Reproduction and life history**

292 Despite its broad distribution range, comparative over-  
 293 views on the life history and reproduction of vendace are  
 294 rare. Vendace is a relatively small, short-lived species with  
 295 a plastic life history strategy (Bøhn et al. 2004; Gregersen  
 296 et al. 2011). Maximum length and age are reported to be  
 297 25–30 cm and 5–7 years, respectively, in the majority of  
 298 lakes (Schultz 1992; Bøhn et al. 2004), although fish older  
 299 than 10 years have been found in single lakes (Salonen  
 300 2004). Age at maturation is between 2 and 5 years, with  
 301 males usually reproducing earlier than females (Sandlund  
 302 1992; Bøhn et al. 2004). An increased investment into  
 303 spawning in cold years with low zooplankton abundance  
 304 has recently been demonstrated (Gregersen et al. 2011).  
 305 Spawning occurs along the shores, usually in 4–10 m  
 306 depth, but spawning depth can vary between 1 and 20 m  
 307 with shallowest spawning observed in the most humic lakes  
 308 (Heikinheimo et al. 2006). Eggs sink to the bottom.  
 309 Vendace spawn between early autumn and early winter  
 310 (late October to November in Scandinavia, December in  
 311 Northeast Germany) at water temperatures of ca. 6–7 °C  
 312 (Koho et al. 1991; Nyberg et al. 2001). Larvae hatch in  
 313 early spring a few days after ice-off in the lakes and spend  
 314 the first 4–6 weeks close to surface, primarily inhabiting  
 315 littoral areas (Karjalainen 1992; Nyberg et al. 2001; Karj-  
 316 alainen et al. 2002; Urpanen et al. 2005). This is assumed  
 317 the most critical phase due to the limited habitat extension  
 318 and hence high density of larvae. Juveniles of 20–30 mm  
 319 length move into the pelagic zone and continue to be  
 320 strictly pelagic over their lifetime. It has to be noted,  
 321 however, that in some lakes, vendace larvae are exclusively  
 322 pelagic already immediately after hatch (Karjalainen et al.  
 323 2002). An early nearshore phase and migration to deeper  
 324 areas at about 15–20 mm fish length has been documented  
 325 also for larval *Coregonus artedii* (summarized by Stockwell  
 326 et al. 2009).

327 Year-class strength (YCS) of mature coregonids can  
 328 vary up to 20-fold (Helminen et al. 1993; Helminen and  
 329 Sarvala 1997; Nyberg et al. 2001; Stockwell et al. 2009),  
 330 whereas even higher inter-annual variation has been doc-  
 331 umented for densities of young-of-the-year (yoy) fish

(Mehner et al. 2011a). Recruitment success of vendace is  
 only moderately proportional to the size of the spawning  
 stock (Helminen et al. 1997; Karjalainen et al. 2000). The  
 abundances of spawners and recruits are best characterized  
 by a compensatory relationship (Valtonen and Marjomäki  
 1988; Marjomäki 2004). In contrast, larval density at age of  
 3 weeks and YCS of mature fish are strongly correlated,  
 indicating that the critical period occurs during the first  
 weeks after hatching (Viljanen 1988; Huusko and Sutela  
 1998; Karjalainen et al. 2000; Marjomäki et al. 2004).  
 Large-scale synchrony in population abundances of core-  
 gonids suggests that there is an important density-inde-  
 pendent mechanism influencing recruitment (Marjomäki  
 et al. 2004; Bunnell et al. 2010), most likely driven by the  
 temperature development during winter and early spring  
 and date of ice break (Nyberg et al. 2001; Mehner et al.  
 2011a).

There is little information available on the life history of  
 sympatric coregonids in European lakes (subsequently  
 referred to as ciscoes, including *C. fontanae*, *C. lucinensis*  
 and *C. trybomi*). These species are characterized by  
 spawning in spring and early summer, with the spawn-  
 ing time extending from late April until July (Table 1).  
*C. fontanae* is smaller than the sympatric vendace in Lake  
 Stöcklin (maximum length about 15 cm) (Anwand et al.  
 1997), whereas *C. lucinensis* (Scharf et al. 2008) and  
*C. trybomi* are presumably only slightly smaller than  
 vendace. Hatching dates and ecology and distribution of  
 early life stages are widely unknown for these species.  
 Adults of spring-spawning species are pelagic and co-occur  
 locally with vendace where sympatric, but may display  
 vertical segregation from vendace (Mehner et al. 2010a).  
 Among the ciscoes from the Great Lakes, only the allo-  
 patric *C. artedii* population of the Lac des Écorces (Quebec,  
 Canada) is a spring-spawner that hatches in later July and  
 has low size after first summer and matures at age 3  
 (Henault and Fortin 1989, 1993). The other ciscoes of the  
 Great Lakes and Siberia are autumn to winter spawners  
 with comparable maximum size or age, and age at matu-  
 ration, as found for vendace (Table 1). Interestingly,  
*C. reighardi* was originally described as spring-spawning  
 species, but a switch towards autumn spawning has been  
 reported in the Great Lakes (Scott and Crossman 1973).

The life history of clupeids in temperate marine systems  
 is well studied. Sprat is a batch spawner and exhibit high  
 spawning activity in different months depending upon the  
 latitude. At the lower latitudinal limit in the Mediterranean  
 (Adriatic) Sea, sprat generally spawns during the  
 winter months (October to April) with peak spawning in  
 November and December at water temperatures between 9  
 and 14 °C (Dulcic 1998). At the northern latitudinal limit,  
 sprat spawns between March and August in the Baltic Sea  
 (Elwertowski 1960; Parmanne et al. 1994; Baumann et al.

**Table 1** Overview on maximum length ( $L_{\max}$ , cm), maximum age ( $A_{\max}$ , years), age at maturity ( $A_{\text{mat}}$ , years), spawning months and dominant diet for temperate and arctic freshwater coregonids inhabiting lakes, and for marine clupeids

Species	$L_{\max}$ (cm)	$A_{\max}$ (y)	$A_{\text{mat}}$ (y)	Spawning months	Diet
<b>Coregonids</b>					
<i>Coregonus albula</i>	25 (43)	6 (19)	2 (5)	Oct–Dec	Planktonic
<i>Coregonus fontanae</i>	15	3	2	Apr–Jul	Planktonic
<i>Coregonus lucinensis</i>	20	6	2	Apr–Jul	Planktonic/benthic
<i>Coregonus trybomi</i>	20	?	?	Apr–May	?
<i>Coregonus artedi</i>	25 (47)	7 (17)	3 (6)	Nov–Dec	Planktonic
<i>Coregonus hoyi</i>	25 (38)	7 (12)	3–4	Dec–Mar	Planktonic/benthic
<i>Coregonus kiyi</i>	25 (35)	7 (10)	3–4	Oct–Dec	Benthic
<i>Coregonus zenithicus</i>	28 (43)	(11)	4–6	Sep–Nov	Benthic
<i>Coregonus reighardi</i>	25 (36)	(8)	?	Oct–Nov (May <sup>a</sup> )	Benthic
<i>Coregonus nigripinnis</i>	33 (39)	(14)	4–5	Sep–Jan	Benthic
<i>Coregonus sardinella</i>	23 (47)	11 (22)	3 (7)	Sep–Nov	Planktonic/benthic
<b>Clupeids</b>					
<i>Clupea harengus</i>	30 (45)	15 (22)	3 (6)	Jan–Dec	Planktonic
<i>Sprattus sprattus</i>	12 (16)	5 (20)	2	Feb–Jul	Planktonic

Average values are given together with maximum reported values (in parentheses) where available. Data were compiled primarily from taxonomic handbooks (Scott and Crossman 1973; Kottelat and Freyhof 2007) and online sources ([www.fishbase.org](http://www.fishbase.org))

<sup>a</sup> *C. reighardi* was considered a spring-spawner according to earlier descriptions (Scott and Crossman 1973)

2006a) and a bit later (May through August) in the North Sea (Wahl and Alheit 1988). Observations in the Baltic detected spawning females as early as January (Haslob et al. 2011), and in 2003, a second spawning peak was observed in autumn, both related to exceptional inflow events of warm North Sea water penetrating deep basins such as the Bornholm Basin (Kraus et al. 2004). Another possible explanation for this second spawning peak is the fact that sprat are able to extend their spawning period by directly channelling energy from food consumption into reproduction and not only relying on the energy stored until maturation (Blaxter and Hunter 1982).

In the Baltic, sprat spawning primarily occurs within deep basins, but occurs in both coastal and offshore waters in the North Sea (Whitehead 1985) and the time of peak spawning, relative fecundity and batch fecundity vary significantly between years and regions (Wahl and Alheit 1988). Batch fecundity is positively correlated with water temperature during the pre-spawning period (Haslob et al. 2011). Salinity changes during the spawning season can modify the buoyancy of the eggs and yolk sac larvae (Petereit et al. 2009). Higher salinity at fertilization increases the specific gravity of eggs and therefore induces a deeper vertical distribution. The resulting variability in vertical distribution can affect the mortality of the sprat eggs by altered temperature and oxygen conditions (Petereit et al. 2008) and a changing overlap of predators and prey. Model simulations by Hinrichsen et al. (2005) have shown that larvae drift to the nearshore juvenile nursery grounds on the Swedish or Polish coastline. The drift

depends on wind direction and forcing thus leading to a mixing of the juveniles from the different spawning stocks. Adult sprat are generally mature at 2 year though some members of the population may spawn at 1 year (Bailey 1982). After the spawning season in the Baltic, adults of sprat leave the deep basins to feed in shallower, coastal waters. Age-0 juveniles join adult schools in the autumn and re-emigrate with adults to the spawning grounds in late winter. In the North Sea, the spawning and migration dynamics of sprat as well as herring can be considered a marine estuarine opportunist strategy (Thiel and Potter 2001; Guelinckx et al. 2006).

Atlantic herring spawns in coastal and shelf regions across the northern Atlantic Ocean while its sister species (Pacific herring, *Clupea pallasii*) spawns in similar habitats throughout the northern Pacific. Atlantic herring displays remarkable flexibility in its spawning phenology utilizing every season depending upon the specific ecosystem such as summer (northern Baltic), spring (Norway), autumn (northern North Sea) and winter (southern North Sea) (see Hufnagl and Peck 2011, their Fig. 7). In the North Sea, four different stocks (Shetland/Orkney, Buchan, Banks, Downs) have been described, which differ in growth rates, migration routes (Harden Jones 1968) and recruitment patterns (Dickey-Collas et al. 2010). In the North Sea, herring show anti-clockwise migration patterns with the fish leaving the overwintering grounds in the eastern North Sea (Norwegian coast) to move westwards to the feeding grounds. Spawning starts on the east coast of Scotland in August/September and continues to September/October for

445 the herring spawning in the Dogger Bank area. October to  
446 January is the spawning time for the Downs and Channel  
447 herring (Harden Jones 1968; Blaxter and Hunter 1982).  
448 Once entrained as juveniles to a spawning ground by  
449 joining migrating adults, the majority of the spawning  
450 group returns to the same grounds from year to year  
451 (homing) (Stephenson et al. 2009).

452 In the eastern North Sea, the Norwegian Sea, the  
453 Skagerrak and the Baltic Sea, spawning primarily  
454 takes place in spring, but with smaller autumn- and  
455 winter-spawning population components occurring locally  
456 (Blaxter and Hunter 1982). Spring spawners also are more  
457 abundant in the western Atlantic herring stocks in colder  
458 waters where the larvae have to grow during summer to  
459 reach the juvenile stage in late summer or autumn.  
460 Autumn spawners in the western Atlantic are found in  
461 southern areas where larvae spent a longer time in colder  
462 winter waters before they reach metamorphosis in spring.  
463 This represents two strategies to cope with different  
464 environments during early development of the offspring  
465 (Messieh 1975; Melvin et al. 2009). In the northwest  
466 Atlantic, herring utilizes spawning areas from Labrador to  
467 Cape Hatteras (Messieh 1988; Safford and Booke 1992;  
468 Armstrong and Cadrin 2001).

469 Autumn spawners mostly deposit eggs on specific  
470 spawning grounds in deeper offshore areas, whereas  
471 spring-spawning herring utilize shallow near-coast habitats  
472 (Klinkhardt 1996). As opposed to sprat, herring are single-  
473 batch spawners spawning only one batch per year in  
474 schools with the composition of the school changing over  
475 time, since individuals appear and disappear from the  
476 spawning ground (Blaxter and Hunter 1982; Axelsen et al.  
477 2000; Skaret et al. 2003; Geffen 2009). Individual females  
478 leave the school, deposit their “sticky” demersal eggs  
479 mainly on plant material (like *Fucus*, *Laminaria*, *Zostera*)  
480 on the sea floor in the Baltic and mainly on gravel and rock  
481 and mussel beds in the North Sea (Geffen 2009) and are  
482 followed by one or more males which fertilize the newly  
483 spawned eggs (Aneer 1982). After spawning, there is a  
484 mixing in the central North Sea when the fish migrate  
485 easterly to the overwintering grounds near the Norwegian  
486 coast and the Skagerrak. Cushing (1975) modified the  
487 “triangle of migration” (Harden Jones 1968) by including  
488 the early life stages and linking their larval drift patterns to  
489 circulation features.

490 Herring show a very flexible life history strategy with  
491 embryos and larvae from these different herring stocks  
492 experiencing different salinities, temperatures and day  
493 lengths as well as predator fields and food availabilities  
494 on their spawning grounds (Klinkhardt 1996; Geffen  
495 2009). The composition of mesozooplankton communities  
496 in the Baltic Sea changes regionally due to differences in  
497 ambient salinity and temperature (Möllmann et al. 2000).

498 Thus, herring and their offspring will be faced with dif-  
499 ferent food sources in the different spawning regions  
500 (Möllmann et al. 2005). Autumn and winter spawners  
501 have larger eggs than spring and summer spawners  
502 (Blaxter and Hempel 1963; van Damme et al. 2009). The  
503 eggs of the spring spawners are larger than those of the  
504 summer spawners, a strategy used to compensate for  
505 the greater variability in the production cycle during the  
506 spring-spawning phase (Blaxter and Hunter 1982). Sur-  
507 vival of the offspring in autumn/winter in a season of low  
508 productivity is possible, since herring larvae are able to  
509 survive long periods of little or no growth and the larger  
510 size of the larvae affects their survival chance (Johann-  
511 essen et al. 2000; Geffen 2009).

## Summary and comparison 512

513 The life histories of coregonids and clupeids are strikingly  
514 similar with both groups maturing early in life, having low  
515 to moderate longevity and maximum sizes not exceeding  
516 about 30–35 cm (Table 1). Likewise, both groups often  
517 utilize nearshore areas for spawning, the eggs of corego-  
518 nids and herring are attached to substrates or sink to the  
519 shallow bottom, and the early larvae can occur in shallow  
520 nearshore areas. The benefit from this benthic spawning  
521 strategy is that growth of the larvae occurs in a very spe-  
522 cific region at a very specific time without large dispersal  
523 losses after long incubation periods (Blaxter and Hunter  
524 1982). After the nearshore phase, older larvae leave their  
525 initial feeding habitat, and either migrate over short  
526 (freshwater coregonids) or passively drift long (marine  
527 clupeids) horizontal distances to their pelagic habitats  
528 where they spend the juvenile and adult phases before  
529 returning to the nearshore habitats for spawning. Baltic  
530 sprat are an exception in that they also utilize offshore,  
531 deeper areas for spawning with larval drift to shallower  
532 areas.

533 Another important characteristic for both groups is that  
534 a high variety of spawning times (from autumn over  
535 winter to spring and early summer) are utilized by distinct  
536 populations (particularly herring and ciscoes) and that  
537 spawning-times appear to have evolved as an adaptation  
538 to intense competition and local conditions at the  
539 spawning grounds (in both groups) or within larval/juve-  
540 nile nursery areas (in clupeids) (Gaggiotti et al. 2009). A  
541 systematic understanding of the correspondence between  
542 spawning time, spawning duration, fecundity and egg  
543 size, larval mortality and the abiotic conditions at the  
544 spawning location (temperature, salinity) might be a  
545 promising research avenue within the framework of the  
546 plasticity of life history strategies in fishes. This approach  
547 could benefit from an explicit comparison of coregonids  
548 and clupeids.

549 **Inter- and intraspecific ecological interactions**

550 Coexisting populations of coregonids have repeatedly been  
551 used as model organisms to study competitive interactions  
552 within the process of ecological speciation (Østbye et al.  
553 2006; Bernatchez et al. 2010; Siwertsson et al. 2010). Most  
554 of these populations follow the typical benthic-pelagic  
555 segregation, but other types of ecological divergence are  
556 also found (reviewed by Hudson et al. 2007). Ecological  
557 segregation along the depth gradient within the pelagic area  
558 is less frequently reported than the benthic-pelagic diver-  
559 gence, but is nevertheless described in a few lakes.  
560 Examples include ciscoes in Lake Nipigon, North America  
561 (Turgeon et al. 1999), and coexisting vendace and white-  
562 fish in Lake Skrukkebukka, northern Norway (Gjelland  
563 et al. 2007).

564 Vendace has a high number of gill rakers and is regarded  
565 a specialist zooplanktivore (Hamrin 1983; Viljanen 1983;  
566 Northcote and Hammar 2006), although recent observa-  
567 tions suggest some flexibility in diet choice (Liso et al.  
568 2011). Due to its efficient zooplankton foraging, vendace  
569 may outcompete and hence exclude other planktivorous  
570 fish species from the pelagic area (Beier 2001; Bøhn and  
571 Amundsen 2001) and cause changes in the zooplankton  
572 community (Karjalainen and Viljanen 1993; Helminen and  
573 Sarvala 1997; Amundsen et al. 2009). A strong influence of  
574 planktivory on the zooplankton community has also been  
575 found for *C. artedi* (Rudstam et al. 1993). Inter-cohort food  
576 competition in vendace populations is strong, in particular  
577 during the warmer summer months, and hence, population  
578 dynamics of vendace in many lakes is characterized by bi-  
579 annual cycles (Hamrin and Persson 1986; Helminen et al.  
580 1993; Helminen and Sarvala 1994; Karjalainen et al. 2000).

581 A recent comparison of several lakes (Kahilainen et al.  
582 2011b) illustrated that the predation efficiency for zoo-  
583 plankton increased with the number of coregonid (vendace  
584 and whitefish) forms that coexist in a lake. Along this  
585 gradient of planktivore efficiency, the zooplankton com-  
586 munities were modified accordingly, resulting in smaller-  
587 sized prey in the lakes containing the most efficient  
588 planktivorous forms with highest number of gill rakers  
589 (Kahilainen et al. 2011b). In contrast, for sparsely rakered  
590 forms, this reduction in prey size has probably reduced the  
591 opportunity to utilize the zooplanktivorous niche in these  
592 lakes. As a result of this eco-evolutionary feedback  
593 between predators and prey, the formation of intermediate  
594 phenotypes has decreased and resource segregation among  
595 the coregonids increased (Kahilainen et al. 2011b). In this  
596 context, almost nothing is known on the competitive  
597 strength of the spring-spawning *Coregonus* species. In  
598 Lake Stechlin, both vendace and Fontane cisco are truly  
599 pelagic and utilize the same planktonic food source  
600 (Helland et al. 2008), suggesting strong exploitative

601 competition. Similar feeding efficiencies for zooplankton  
602 in vendace and Fontane cisco from Lake Stechlin  
603 (Ohlberger et al. 2008a) suggest no advantage of vendace  
604 over cisco in exploiting pelagic zooplankton resources.

605 Competition and niche partitioning between the  
606 North-American ciscoes in the Great Lakes have not been  
607 thoroughly studied, but recently Gamble et al. (2011a)  
608 simulated a food web of the pelagic fish community in  
609 Lake Superior. This study showed that the dominant  
610 planktivores in the lake are cisco (*C. artedi*) and kiyi  
611 (*C. kiyi*). Additionally, a third coregonid species, bloater  
612 (*C. hoyi*), also inhabits the pelagic area. In spite of some  
613 seasonal variations, the three species appear to largely  
614 overlap in diet, with *Mysis* as the most important prey,  
615 similar to the dominance of *Mysis* in the diet of *C. lucinensis*  
616 in the German Lake Breiter Luzin (Scharf et al. 2008). Yet,  
617 cisco has a more flexible diet compared to the other species  
618 which includes more calanoid copepods, *Daphnia* and  
619 *Bythotrephes* (Gamble et al. 2011a). This is probably rela-  
620 ted to the fact that cisco also exhibits more variation in the  
621 seasonal diel migration than the other coregonids. Another  
622 recent study examined trophic niche partitioning among all  
623 deepwater coregonids in the Great Lakes, based on stable  
624 isotopes of both historical and contemporary data (Schmidt  
625 et al. 2011). These results indicate that within all lakes,  
626 individual species have occupied distinct ecological niches.  
627 The ecological distinctness has been dynamic, but yet  
628 maintained over time in spite of ecological disturbances.  
629 The study suggests that segregation in habitat depth seems  
630 to be the major driver of the niche divergence among  
631 coregonids in the Laurentian Great Lakes.

632 Great Slave Lake, Canada, consists of several coregonid  
633 populations that have remained more intact compared to  
634 those in the Laurentian Great Lakes, thanks to fewer  
635 human-induced changes. Also here the taxonomy is not  
636 resolved, and the ecological diversity is not well described.  
637 It seems, as if the lacustrine cisco (*C. artedi*) might have  
638 overlapping diet or habitat with some of the other forms  
639 in the pelagic area (Muir et al. 2011). In Barrow Lake,  
640 Canada, cisco is reported to coexist with shortjaw cisco  
641 (*C. zenithicus*). Shortjaw cisco mainly eats *Mysis*, and only  
642 limited amounts of copepods and cladocerans (Steinhilber  
643 et al. 2002).

644 Also in marine environments, pelagic clupeids are  
645 known to influence zooplankton dynamics, which conse-  
646 quently regulate competitive interactions among planktiv-  
647 orous fishes. For example, variations in herring condition  
648 have been explained by plankton availability, partly regu-  
649 lated by both intraspecific (density-dependence) and  
650 interspecific competition with sprat (Möllmann et al. 2005;  
651 Casini et al. 2010). Sprat is a strict zooplanktivorous spe-  
652 cialist, while herring may feed upon zooplankton and  
653 benthic food organisms as large juveniles and adults.

Hence, the interspecific competition between sprat and herring is likely strongest at smaller size (Casini et al. 2004). However, the diet overlap between herring and sprat does not only change ontogenetically, but also varies seasonally and with prey abundance and composition (Casini et al. 2004).

As mentioned above, ecological divergence and local adaptations seem to be highly important in both freshwater coregonids and marine clupeids, and in both systems genetically distinct spawning populations likely have resulted, at least in part, from competitive interactions. However, while comparisons of sympatric populations of coregonids mostly have focused on variation in feeding habitat resulting from competition among adults, studies of sympatric herring populations have mainly described variation in spawning behaviour, probably related to competition between younger stages. Although a comprehensive mechanistic understanding has not yet been achieved, it has been proposed that competition for a suitable substratum for eggs and for food among larvae could be involved in the spawning time divergence in herring (Jørgensen et al. 2005).

A similar competition among younger life stages may have been important in the development of the segregated spawning periods between the coregonids in Lake Stechlin (Helland et al. 2008, 2009). Although adults of vendace and Fontane cisco show only subtle ecological differences, their larvae most likely share much less ecological similarities. Because the larvae of the two species hatch at different times of the year, autumn- and spring spawners probably face highly dissimilar environments (e.g. temperature, predation risk, food abundance) during their first weeks of life (Nyberg et al. 2001). Development of reproductive isolation in sympatry cannot happen without simultaneous reduction in the competition, to allow the divergent populations to coexist (Coyne and Orr 2004). Asynchrony in timing of spawning and hatching may contribute directly to the coexistence of sympatric populations, through temporal partitioning of resources and habitat.

Predatory interactions are functionally similar for coregonids and clupeids. Substantial mortality of coregonids is found during the larval phase, primarily induced by perch (*Perca fluviatilis*) predation (Helminen and Sarvala 1994; Huusko et al. 1996). Juvenile and adult coregonids are important prey items of the few pelagic piscivores, such as perch, brown trout (*Salmo trutta*) or lake trout (*Salvelinus namaycush*) (Heikinheimo 2001; Valkeajärvi and Marjomäki 2004; Hrabik et al. 2006; Gamble et al. 2011a, b).

Cod is the main predator on sprat and herring in the Baltic Sea (Sparholt 1994). It could be shown that sprat and herring stocks substantially benefited from the decreased predation pressure imposed by cod and from concurrently

low rates of fishing mortality (Köster et al. 2003). In the Baltic Sea, predation on eggs of herring and sprat is temporally variable and seems to depend upon the extent of vertical overlap between adults and eggs (Köster and Möllmann 2000a, b). Sprat larvae were only occasionally discovered in low numbers in the stomachs of clupeid (herring and sprat) predators, suggesting low predation mortality of larvae by clupeids (Köster and Möllmann 1997). The feeding impact of medusae and chaetognaths on fish early life history stages in the Baltic is also very low (Barz and Hirche 2005). Another predator for sprat in the Baltic are piscivorous seabirds, for example the common guillemot *Uria aalge* that directly affects the sprat population in the Baltic and is indirectly affected by the fishery strategies on sprat and cod (Österblom et al. 2006).

In marine systems, herring and sprat form important trophodynamic links between lower (zooplankton) and upper (piscivores) trophic levels. In different regions, the populations of both sprat and herring exhibit out of phase oscillations with populations of their key predators suggesting strong top-down control. Examples of this tight coupling between populations of sprat and herring and those of gadoid predators include sprat and Atlantic cod (*Gadus morhua*) in the Baltic Sea and herring and haddock (*Melanogrammus aeglefinus*) on Georges Bank in the northwest Atlantic (Richardson et al. 2011). Although heavily exploited in fisheries, multispecies virtual population analyses suggest that removal of these clupeids by predators exceeds that by commercial fisheries (Tyrrell et al. 2008).

Similarities between coregonids and clupeids can be found also with respect to host–parasite interactions. The dominant parasites of coregonids are cestodes, primarily transmitted via copepods that are part of the planktonic diet of coregonids (Hoff et al. 1997; Pulkkinen et al. 1999; Pulkkinen and Valtonen 1999). In Atlantic herring, 41 marine parasite species including metacercaria, nematodes and gastrointestinal trematodes were found (Arthur and Arai 1984; MacKenzie 1987). Transmission of most of these parasites seems to be restricted to the coastal waters. Tolonen and Karlsbakk (2003) studying the parasitic assemblage in Norwegian spring-spawning herring found very similar assembly as in other North Atlantic fish stocks. In Baltic herring, 31 parasitic species have been recorded and 23 species in the North Sea (MacKenzie 1987). Parasitic infestation with the larvae of *Anisakis simplex* (nematode) was shown for sprat and herring in the Baltic Sea varying significantly with geographical region. Highest infection rates were found in areas of low salinity, low temperature and reduced oxygen conditions. Sprat was less affected than herring (Grygiel 1999) indicating differences in susceptibility to diseases between herring and sprat. Endoparasitic infections with metacercaria, larval

760 nematodes and larval cestodes in herring were analysed for  
761 their use in stock identifications. The study showed a  
762 remarkable stability in the parasite fauna over time and  
763 showed a significant difference in the prevalence and  
764 infection of the parasite infracommunities validating the  
765 use of parasites as biological tags and as a method for stock  
766 discrimination (Campbell et al. 2007).

767 In the North Sea, herring larvae are known to suffer  
768 mortality due to both endo- and ectoparasites including  
769 nematodes and cestodes, and certain copepod species,  
770 respectively (Rosenthal 1967). Heath and Nicoll (1991)  
771 reported that larvae infected by the cestode (*Scolex pleu-*  
772 *ronectis*) had nearly a 50 % reduction in feeding incidence  
773 (24 %) compared to those that did not contain endoparasites  
774 (44 %). Furthermore, no larvae smaller than 15 mm  
775 contained these endoparasites, whereas incidences of  
776 infection increased with increasing body size in larvae  
777 >15 mm and were highest in coastal waters. Those authors  
778 speculated that this biological mechanism may interact  
779 with changes in drift trajectories to affect YCS of herring in  
780 the North Sea. More recent work (Lusseau et al. 2009)  
781 utilized the prevalence of endoparasites as an index of  
782 larval feeding incidence, overwinter survival and YCS.

### 783 Summary and comparison

784 In both clupeids and coregonids, planktivory is the dominant  
785 feeding strategy, although single populations may show  
786 locally deviating strategies with an enhanced uptake  
787 of benthic animals or even fish. However, a complete  
788 switch to benthivory, as often observed in one of the  
789 coexisting freshwater whitefish populations, has been  
790 documented only in the deepwater forms of *C. artedii* s.l  
791 of the Great Lakes (Table 1). Therefore, there is a fixed  
792 connection of niche dimensions between pelagic habitat  
793 use and planktonic feeding strategy. The dominant plank-  
794 tivory may intensify intra- and interspecific competition  
795 because there is no further specialization and niche seg-  
796regation possible (in contrast to the variety of benthivorous  
797 or piscivorous feeding strategies). This limited niche seg-  
798regation along the diet axis in the pelagic habitat may  
799 contribute to forced microhabitat segregation along the  
800 depth and temperature gradients as found in pelagic core-  
801gonids. However, it may also explain why divergent  
802 selection operates primarily on the early life stages in both  
803 groups. The result, spawning-time switching, might be the  
804 most efficient strategy to reduce competition by avoidance  
805 of simultaneous occurrence of comparable life history  
806 stages and similar-sized individuals. The primarily pelagic  
807 life style of coregonids and clupeids also results in pred-  
808ator-prey and host-parasite interactions that are functionally  
809 comparable. There is growing evidence that these ecolog-  
810ical interactions likewise contribute to local adaptation of

populations (Fraser et al. 2011). However, these interac-  
tions and their correspondence to ecology and life history  
of the species are much better studied in the marine than in  
the freshwater species.

### Behavioural ecology

Diel vertical migration (DVM), one of the most striking  
patterns of rhythmic population behaviour, has been  
repeatedly documented from planktivorous coregonids.  
The regular DVM consists of the occurrence of fish in  
relatively dark and cold hypolimnetic areas during day-  
time, an ascent into warmer metalimnetic waters during  
dusk, a night-time occurrence in metalimnetic waters, and  
a descent back into deep layers during dawn. DVM in  
coregonids has been reported from several lakes (Dem-  
binski 1971; Hamrin 1986; Hrabik et al. 2006; Stockwell  
et al. 2010). Ascent and descent are proximately triggered  
by the change of illumination threshold during dusk and  
dawn (Jurvelius and Marjomäki 2008; Busch and Mehner  
2009). The ultimate causes of coregonid DVM have  
been widely discussed with some controversy, but most  
researchers suggest that fish leave the well-lit near-surface  
layers during daytime to avoid visually oriented predators  
(Hrabik et al. 2006; Gjelland et al. 2009). Interestingly,  
however, evidence for high predation risk of coregonids in  
shallower layers of lakes could rarely be found, because the  
density of piscivores was in most cases surprisingly low  
(Hrabik et al. 2006; Stockwell et al. 2010; Mehner et al.  
2010a). Therefore, a genetically fixed migration has been  
discussed as a response to the 'ghost of predation past'  
(Mehner et al. 2007b; Jurvelius and Marjomäki 2008).

An additional ultimate cause of DVM was put forward  
for the coregonids of Lake Stechlin, where hydroacoustic  
observations of population depths at night revealed strong  
seasonal fluctuations, with fish occurring in deeper water in  
spring and autumn than during the summer months  
(Mehner et al. 2005, 2007b). There was a significant cor-  
relation between population depths and vertical tempera-  
ture gradients (Mehner et al. 2007b; Busch and Mehner  
2009), suggesting that fish seek layers with metabolically  
optimum temperatures at night (Mehner et al. 2010a).  
However, a bioenergetics benefit of DVM for Lake  
Stechlin coregonids could not be demonstrated. Busch  
et al. (2011) used a bioenergetics model to explore that the  
regular DVM is not the most efficient strategy. They sug-  
gested that multiple factors, rather than bioenergetics effi-  
ciency alone, are the evolutionary basis to explain DVM. In  
addition, no growth advantage (that should be expected  
when bioenergetics efficiency is assumed to drive DVM)  
was found for vendace switching in experiments between  
high and low temperatures relative to fish held at constant

861 temperatures (Mehner et al. 2011c). However, fish per-  
862 forming DVM may benefit from predation avoidance  
863 without compromising their metabolic balance and hence  
864 growth rates (Mehner et al. 2011c).

865 Regular DVM is also well described from populations of  
866 Atlantic herring and sprat in the North and Baltic Seas  
867 (Nilsson et al. 2003; Cardinale et al. 2003; Axenrot et al.  
868 2004; Orłowski 2005). The utilization of DVM by sprat in  
869 the Baltic appears to have changed in the last decade.  
870 Previously (in the 1990s), sprat larvae in the Bornholm  
871 Basin performed a normal DVM, being captured during the  
872 day in deeper water layers (e.g. below the thermocline,  
873 40 m) and at night in surface waters. In contrast, a con-  
874 sistent lack of DVM was observed when sprat were  
875 re-sampled in the same system from 2002 to 2005 (Voss  
876 et al. 2007). The lack of DVM in recent years is hypoth-  
877 esized to be due to changes in the abundance of copepod  
878 species that have different depth preferences. Specifically,  
879 the abundances of *Acartia* and *Temora* species which  
880 prefer warmer, surface waters have increased, whereas the  
881 abundance of *Pseudocalanus* which inhabits deeper,  
882 colder, more saline depths has decreased (Voss et al. 2007).  
883 Biophysical modelling results of larval feeding and growth  
884 that included these decadal changes in prey fields and water  
885 temperatures suggested fitness benefits related to the  
886 change in larval DVM behaviour (Hinrichsen et al. 2010).  
887 Modelled larvae that maintained the originally normal  
888 DVM in recent years could not meet energy requirements  
889 due to the poor foraging environment at depth.

890 A variety of mechanisms have been proposed to modify  
891 DVM of herring larvae such as hydrographic characteris-  
892 tics (mixed or stratified water body), tidal influences  
893 (Stephenson and Power 1988), the combination of light and  
894 turbulence (Heath et al. 1988), dependency of light and  
895 food availability (Munk et al. 1989) and predator-prey  
896 relationships (Bailey and Houde 1989; Houde 1989). For  
897 North Sea herring, Heath et al. (1991) and Haslob et al.  
898 (2009) observed that herring larvae had a distinct vertical  
899 migration to upper water layers during the day and more  
900 homogenous depth distribution during the night with larger  
901 larvae showing a more pronounced behaviour. The size-  
902 dependent vertical distribution pattern of the herring  
903 appears to be due to the vertical distribution of their prey  
904 organisms (Munk et al. 1989). Since herring larvae are  
905 visual predators that cannot feed at low light intensities  
906 (Blaxter 1962), they have to swim to the upper water layers  
907 to be able to feed, a behaviour that will be influenced by the  
908 degree of mixing or stratification present within the water  
909 column. During the summer in deep Baltic basins, the  
910 adults of both sprat and herring perform DVM with fish  
911 moving towards surface layers (upper 20 m) at dusk and  
912 back to daytime depths of 60–80 m at dawn (Stepputtis  
913 2006).

Reverse migration patterns with an ascent into shallower 914  
layers during dawn and a descent during dusk have recently 915  
been documented for young-of-year herring in a brackish 916  
bay of the Baltic Sea (Jensen et al. 2011). Furthermore, the 917  
vertical distribution at midday was bimodal, suggesting 918  
two alternative migration strategies in these small herring, 919  
somehow similar to a pattern found in coregonids in Lake 920  
Stechlin (Mehner and Kasprzak 2011). Similar to the larval 921  
sprat example, the change in DVM pattern was consistent 922  
with bioenergetics-based predictions of net energy gain. In 923  
the case of herring, the occurrence in warmer water during 924  
the daytime facilitated rapid digestion at intense feeding 925  
phase, whereas herring do not feed at night and hence save 926  
energy by descending into colder layers (Jensen et al. 927  
2011). These bioenergetics-based explanations of behav- 928  
ioural patterns are expanded upon in the next section. 929

## Summary and comparison 930

Diel vertical migrations are common behavioural strategies 931  
in both coregonids and clupeids. This commonality sug- 932  
gests that the vertical gradients of the pelagic habitats in 933  
both freshwater and marine ecosystems create comparable 934  
selective forces on habitat-choice behaviour. The primary 935  
gradients triggering DVM seem to be illumination strength 936  
as the proximate factor, and temperature that may be 937  
considered as both proximate (guiding the fish into pre- 938  
ferred habitats) (Levy 1990) and ultimate (fitness advan- 939  
tage at increased bioenergetics efficiency of growth) (Brett 940  
1971) factor. However, vertical distributions of prey, intra- 941  
and interspecific competitors, and predators are locally 942  
variable, and hence, a single unique evolutionary causation 943  
of DVM across all populations and habitats cannot be 944  
achieved. In turn, this variety of local conditions may 945  
explain why DVM patterns have been found to be both 946  
seasonally and annually highly variable in some of the 947  
studied populations and may respond to drastic change in 948  
environmental factors (Hinrichsen et al. 2010). The indi- 949  
vidual variability within population-wide migration pat- 950  
terns and its evolutionary causation has just started to be 951  
explored (Mehner and Kasprzak 2011). During early 952  
ontogeny, physostome fishes such as clupeids and core- 953  
gonids must ascend to surface waters and gulp air to fill 954  
their swim bladders. Thus, ontogenetic changes in depth 955  
distribution are also related to this functional, morpholog- 956  
ical constraint (Blaxter and Batty 1984). 957

## Physiological ecology 958

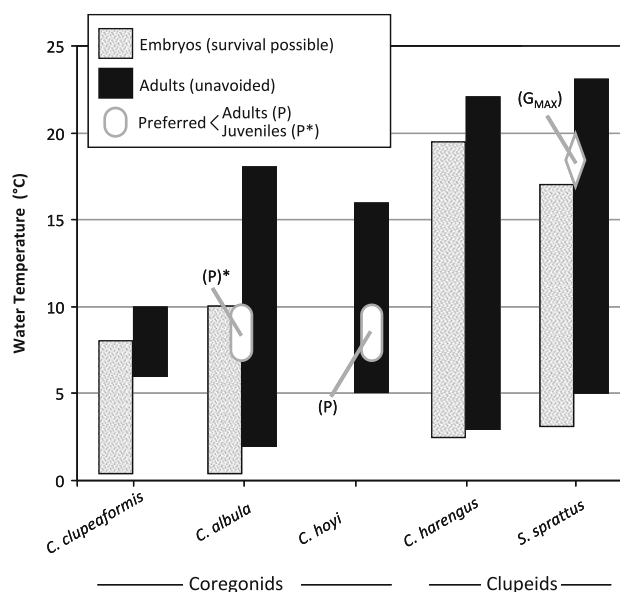
Abiotic gradients contribute to the structuring of freshwater 959  
and marine fish assemblages. Factors of major interest are 960  
temperature and oxygen, and additionally salinity in 961



962 marine ecosystems. Ecological specialization along these  
 963 gradients in response to strong competition involving traits  
 964 not related to feeding strategies has been discussed to  
 965 contribute to speciation in fishes (Mehner et al. 2011b).  
 966 Often, these traits are directly or indirectly related to  
 967 spawning time and location, thermal habitat use and  
 968 energetic trade-offs.

969 Vendace and Fontane cisco in Lake Stechlin display an  
 970 ecological and physiological segregation with respect to  
 971 water depth and thermal habitats, which is as well asso-  
 972 ciated with differences in spawning time. The sister spe-  
 973 cies show differences in metabolic rates with respect to  
 974 temperature (Ohlberger et al. 2008b) and thermal prefer-  
 975 ences (Ohlberger et al. 2008c) that correspond to the  
 976 ecological divergence in habitat use (Helland et al. 2007,  
 977 2008) and suggest different energetic strategies. Ohlberger  
 978 et al. (2012) demonstrated that the scaling of metabolic  
 979 rate with body mass is temperature-dependent in both  
 980 vendace and Fontane cisco in contrast to other species.  
 981 This intra-specific temperature dependence of metabolic  
 982 rates most likely represents a plastic response of energy  
 983 metabolism to the changing thermal conditions and sug-  
 984 gests a more pronounced competitive superiority of small  
 985 compared to large individuals at lower temperatures.  
 986 Differences in size-dependent competition may thus be  
 987 related to the species' thermal habitats (Ohlberger et al.  
 988 2012). Ciscoes in the Great Lakes occupy different water  
 989 depths and can be grouped into pelagic (*C. artedi*, in part  
 990 *C. hoyi*) and deepwater phenotypes (*C. kiyi*, *C. zenithicus*,  
 991 *C. reighardi*, *C. nigripinnis*), corresponding to their pri-  
 992 mary diet (Table 1). The adaptive diversification of the  
 993 deep-water ciscoes is associated with different physio-  
 994 logical abilities to occupy different water depths, which  
 995 has been related to body size, mass-specific metabolic  
 996 rates and buoyancy characteristics (Clemens and Craw-  
 997 ford 2009).

998 Thermal windows supporting the survival of embryos  
 999 in the laboratory as well as threshold (warm and cold)  
 1000 temperatures avoided by adults in the field have been  
 1001 investigated in coregonids (Dembinski 1971; Crowder and  
 1002 Crawford 1984; Hamrin 1986; Tapaninen et al. 1998) and  
 1003 clupeids (Reid et al. 1996; Peck et al. 2012) (Fig. 2).  
 1004 Embryos of coregonids such as *C. clupeaformis* and  
 1005 *C. albula* can tolerate colder temperatures but have more  
 1006 narrow thermal windows compared to both the embryos  
 1007 of both clupeids considered in this review (sprat and  
 1008 herring). Adult clupeids can exploit a wider range of  
 1009 water temperatures and can grow well at warmer tem-  
 1010 peratures than adult coregonids. Preferred temperatures  
 1011 often coincide with those optimal for growth (e.g. Jobling  
 1012 1981), but this depends heavily upon the acclimation  
 1013 characteristics of specific populations (e.g. Pörtner and  
 1014 Peck 2010). Temperatures preferred by juvenile (P\*)



**Fig. 2** Thermal windows supporting the survival of embryos in the laboratory as well as threshold (warm and cold) temperatures avoided by adults in the field for three species of coregonids and two species of clupeid fishes. The range in temperatures preferred by juvenile or adult coregonids and that corresponding to maximum growth (in sprat) are also indicated. Data sources are listed in the text

*C. albula* and adult (*P*) *C. hoyi* (8–10 °C) are half those at which sprat juveniles obtained maximum growth rates ( $G_{MAX}$ ) in the laboratory and field (Peck et al., unpubl. manuscript) (see Fig. 2). This brief review of the thermal constraints of *Coregonus* congeners and clupeids (sprat and herring) reinforces the notion that the life stages of coregonids are more constrained to colder water habitats compared to these clupeids but that both groups display ontogenetic expansion of thermal habitat during the late larval/early juvenile phase and have similar thermal ecologies at spawning (e.g. preferred/optimum at 8–12 °C).

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Both clupeids tolerate a wide range of salinities and hence are both abundant in brackish waters of the Baltic Sea and marine waters of the North Atlantic. The transition zone between the North Sea and the Baltic Sea is an area with a strong salinity gradient spanning from 30 to 34 ‰ in the North Sea to 6–8 ‰ in the Baltic proper, with levels decreasing even down to 3 ‰ in the innermost (north-eastern) parts of the Baltic (Gaggiotti et al. 2009). Thus, changes in salinity levels may shape fish growth rates both indirectly by changing the zooplankton community structure and abundance and/or directly via effects on growth physiology and metabolism (Cardinale et al. 2002). It appears likely that adaptation to the varying salinity at the spawning location contributes to ecological divergence between herring populations, but there are no physiological studies to support this hypothesis.

## 1043 Summary and comparison

1044 The study of metabolic divergence of coexisting pelagic  
1045 populations requires further investigations, because tem-  
1046 perature seems to be important for vertical micro-habitat  
1047 segregation, bioenergetics efficiency of growth, body size  
1048 and life history. It would be promising to explore whether  
1049 temperature conditions during spawning season and at  
1050 spawning location, egg size, growth rate, size at maturation,  
1051 maximum size, optimum metabolic temperature and  
1052 final temperature preferendum correspond across the  
1053 coregonid and clupeid populations of the temperate zone.  
1054 This would suggest a functional interaction between life  
1055 history, metabolism and environmental conditions, as  
1056 recently proposed (Killen et al. 2010).

1057 **Potential effects of climate change**

1058 Studies addressing the effects of global climate change on  
1059 coregonids in lakes are relatively rare (Magnuson et al.  
1060 1990; Elliott and Bell 2011). It is generally assumed that  
1061 the thermal guild of cold-water stenothermal fish to which  
1062 coregonids belong is most vulnerable to global warming  
1063 (Graham and Harrod 2009). This assumption is primarily  
1064 based on the predicted decline of suitable habitats for  
1065 coregonids in lakes due to warming and de-oxygenation of  
1066 deeper water layers (Jacobson et al. 2010; Elliott and Bell  
1067 2011). Nyberg et al. (2001) discussed that the YCS of  
1068 autumn-spawning coregonids whose larvae hatch in early  
1069 spring is expected to decline with warming, whereas the  
1070 YCS of spring spawners might increase because the later-  
1071 hatching larvae of spring spawners can more precisely  
1072 match the temporally shifting peak of zooplankton prey in  
1073 late spring. The coexisting coregonid species in Lake  
1074 Stechlin were an appropriate study system to test this  
1075 assumption. In contrast to the prediction, densities of  
1076 young-of-the-year vendace in June were higher after warm  
1077 winters. However, metalimnetic temperatures in June  
1078 affected densities of juvenile and adult vendace and Fontane  
1079 cisco in opposite direction. Cisco densities were  
1080 higher in warm years, whereas high vendace densities were  
1081 primarily found when June temperatures were cold.  
1082 Metalimnetic temperatures seem to modify the competition  
1083 strength between the interacting coregonids, because high  
1084 densities of cisco forced vendace to occupy shallower and  
1085 hence warmer waters at night, whereas high vendace  
1086 densities forced cisco to stay deeper and hence in too cold  
1087 water (Mehner et al. 2011a).

1088 By using a coupled lake physics and bioenergetics  
1089 model, growth rates of vendace and Fontane cisco were  
1090 simulated for a predicted global change scenario in the year  
1091 2100 (Busch et al. 2012). Two behavioural strategies were

distinguished, with coregonids either performing behav- 1092  
ioural thermoregulation (keeping their temperatures at 1093  
night constant), or fish performing migrations with fixed 1094  
amplitudes (keeping their depth at night and hence illum- 1095  
ination threshold constant). In almost all simulations, 1096  
coregonids were predicted to increase their growth rates, 1097  
even by assuming that zooplankton densities might decline 1098  
by about 10 %. The reason for this unexpected outcome is 1099  
the opposed temperature development of hypolimnetic and 1100  
metalimnetic water layers in Lake Stechlin predicted for the 1101  
warming scenario. Whereas epi- and metalimnetic layers 1102  
between 0 and 18 m will warm, layers deeper than 20 m will 1103  
cool down by up to one degree. Accordingly, fish will 1104  
experience colder water during their daytime residence that 1105  
reduce their metabolic expenditures, and the energy saved 1106  
will more than balance the slightly reduced feeding rates 1107  
from the lower prey densities. However, if fish would follow 1108  
behavioural thermoregulation under these warming condi- 1109  
tions and keep their currently observed temperatures at night, 1110  
their vertical microhabitat segregation will completely col- 1111  
lapse because layers with preferred temperatures for vendace 1112  
and cisco will then largely overlap. Accordingly, tempera- 1113  
ture development of the main habitats is coupled with biotic 1114  
interaction strength, a pattern that has only recently emerged 1115  
as a main research area (Kordas et al. 2011). 1116

1117 Clupeid fish have been one of the best bio-indicators of 1117  
climate-driven changes in marine systems, exhibiting 1118  
strong changes in stock size and distribution because of 1119  
their short lifespan and tight coupling to zooplankton 1120  
dynamics and mesoscale hydrodynamic features sensitive 1121  
to physical forcing (Lluch-Belda et al. 1992; Alheit et al. 1122  
2005; Tourre et al. 2007). Similar to the climate discussion 1123  
of coregonids in lakes, climate change will affect sprat and 1124  
herring (and other marine fish) in both direct and indirect 1125  
ways. Direct effects include changes in water temperature, 1126  
causing species-specific impacts due to differences in 1127  
thermal windows supporting growth and survival (Pörtner 1128  
and Peck 2010). Sprat occurs at the northern boundary of 1129  
its geographical distribution in both the Baltic and North 1130  
Seas suggesting that additional warming (when considered 1131  
in isolation of other factors) would benefit these popula- 1132  
tions (MacKenzie and Köster 2004). On the other hand, at 1133  
its lower latitude limit, sprat has shown dramatic declines 1134  
in recent decades such as the disappearance of the 1135  
spawning population in the Northwest Mediterranean 1136  
(Calvo et al. 2011). These changes are consistent with the 1137  
inter-stock, dome-shaped relationship between recruitment 1138  
and water temperature experienced during spawning 1139  
(MacKenzie and Köster 2004). Herring, which occurs with 1140  
sprat at the lower latitudinal extent of its range in the North 1141  
and Baltic Sea, will also likely experience losses in the 1142  
productivity of specific spawning stocks in southern 1143  
regions due to climate warming (as discussed below). 1144

1145 Compared to lake systems, climate change may have  
 1146 potentially more complex impacts in open marine systems  
 1147 due to losses in connectivity between key habitats. Many  
 1148 marine fish, including clupeids, have evolved complex life  
 1149 history strategies that help promote philopatry, habitat  
 1150 connectivity, life cycle closure and population persistence  
 1151 (Harden Jones 1968; Sinclair 1988). Herring displays  
 1152 spawning site fidelity, an adaptive strategy that has likely  
 1153 evolved to place progeny within environments providing  
 1154 favourable transport to areas promoting high rates of  
 1155 feeding, growth and survival during early life (Cushing  
 1156 1975). Sprat also displays specific preferences for  
 1157 spawning areas such as deep Baltic Basins and the  
 1158 German Bight in the southern North Sea. The YCS of  
 1159 sprat, herring and other marine clupeids has been corre-  
 1160 lated to atmospheric climate oscillations such as in the  
 1161 North Atlantic (NAO) and Pacific (PDO) (Gröger et al.  
 1162 2010). These oscillations are not only highly correlated to  
 1163 changes in water temperature but also the strength and  
 1164 direction of regional wind fields causing changes in the  
 1165 drift trajectories of early life stages (Peck et al. 2009),  
 1166 potentially disrupting the connectivity between essential  
 1167 habitats. In the Baltic, sprat year-class strength has been  
 1168 strongly and significantly correlated to the spawning stock  
 1169 biomass and a drift index (Baumann et al. 2006b) with  
 1170 high year classes resulting when larvae are retained near  
 1171 spawning grounds. Recent biophysical modelling work on  
 1172 sprat in the North Sea comparing different NAO years  
 1173 predicted very little change in potential larval survival;  
 1174 despite differences in drift trajectories and water tem-  
 1175 peratures North Sea sprat larvae matched well (spatially  
 1176 and temporally) with modelled prey fields (Daewel et al.  
 1177 2008).

1178 In North Sea herring, year-class success of autumn  
 1179 spawners appears to be regulated by processes acting  
 1180 during the early life, as larvae drift from western spawning  
 1181 grounds to eastern juvenile nursery areas (Nash and  
 1182 Dickey-Collas 2005). Using a physiology-based foraging  
 1183 and growth model constructed for larval herring, Hufnagl  
 1184 and Peck (2011) estimated the ability for herring to switch  
 1185 spawning times (or spawning areas) in response to climate-  
 1186 driven changes in key factors (temperature, prey fields).  
 1187 The model suggested that climate-driven changes in bot-  
 1188 tom-up factors will affect spring- and autumn-spawned  
 1189 herring larvae in different ways. It is unlikely that autumn-  
 1190 spawning herring will be able to avoid unfavourable con-  
 1191 ditions by delaying their spawning time or by utilizing  
 1192 more northern spawning grounds because of limitations in  
 1193 day-length to larval growth and survival. Conversely, for  
 1194 spring spawners, the success of earlier or later spawning  
 1195 will be tightly constrained by match–mismatch dynamics  
 1196 between larvae and their zooplankton prey (Hufnagl and  
 1197 Peck 2011).

## Summary and comparison

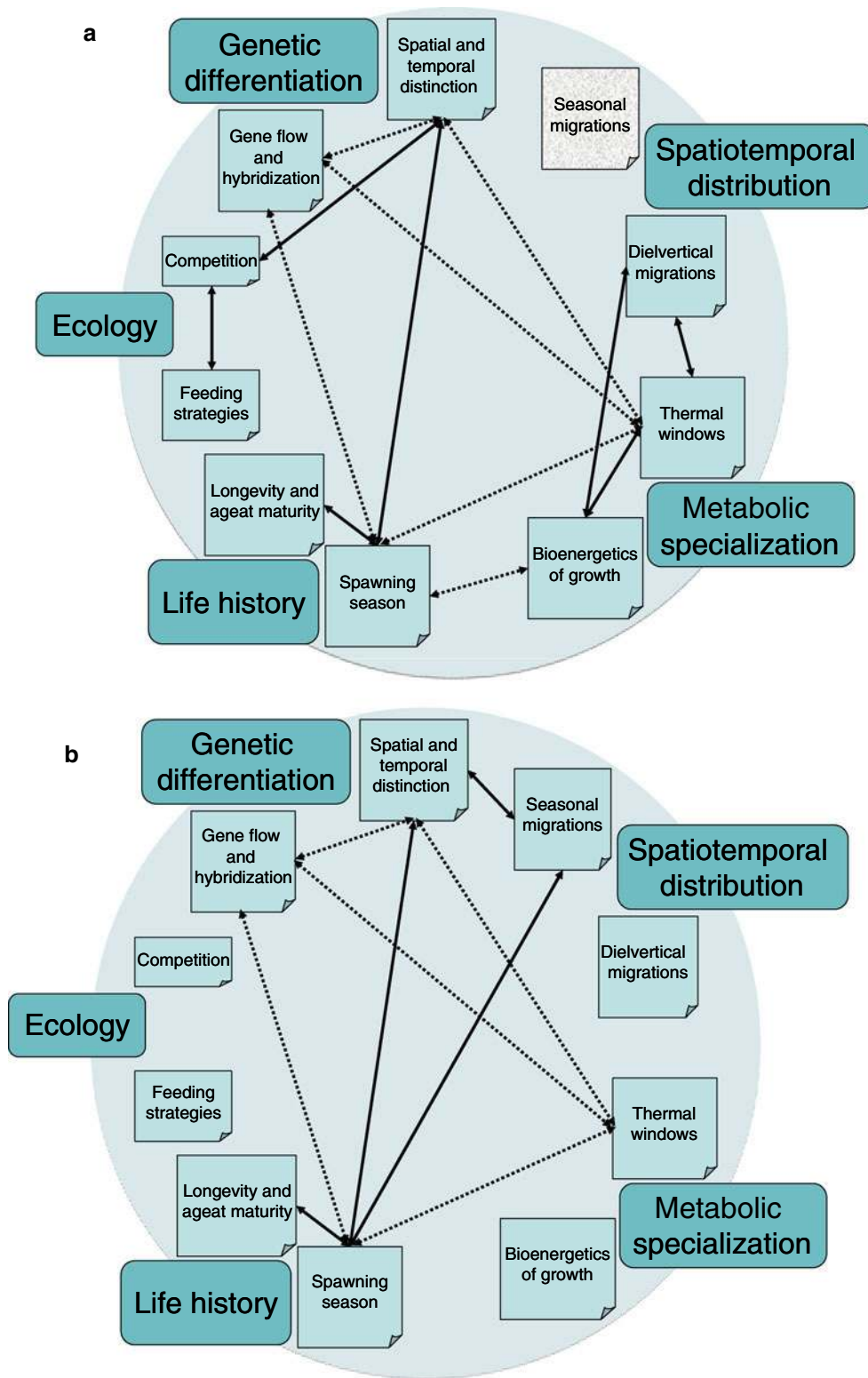
1198  
 1199 Climate warming may affect both fish groups comparably.  
 1200 The most sensitive ontogenetic stages seem to be the fish  
 1201 larvae because of their exposed nearshore habitats in which  
 1202 changes in temperature will occur more pronouncedly than  
 1203 in the much larger pelagic volumes of lakes and seas (see  
 1204 Mehner 2000). Furthermore, volumetric densities of larvae  
 1205 are highest, their daily food demand is highest during  
 1206 ontogeny, and their ability to detect and avoid predators is  
 1207 poorly developed (Houde 1987; Mehner and Thiel 1999;  
 1208 Bochdansky et al. 2008). Therefore, abiotic and biotic  
 1209 factors at nearshore habitats that respond to global warm-  
 1210 ing will have the strongest effect on year-class strengths of  
 1211 coregonids and clupeids, in particular because early life  
 1212 stages have narrower thermal windows than juvenile or  
 1213 adult fish (Pörtner and Peck 2010). For the marine clupeids,  
 1214 the passive transport of late larvae to their juvenile habitats  
 1215 over large distances might be another important phase that  
 1216 can presumably be neglected in coregonids due to the  
 1217 immediate connection of nearshore and pelagic habitats in  
 1218 lakes. Given the potential decline of suitable thermal  
 1219 habitats and limited dispersal opportunity, coregonids in  
 1220 lakes will face changes in competitive interactions and  
 1221 competition strength with changes in the thermal regime  
 1222 (Mehner et al. 2011a).

1223 Because warming may modify autumn, winter and  
 1224 spring seasons differently, the variability of spawning  
 1225 times will cause a response that is specific to each popu-  
 1226 lation. In this context, spring-spawning herring seem to be  
 1227 more robust against warming, a pattern that was predicted  
 1228 also for freshwater spring spawners relative to the more  
 1229 vulnerable autumn spawners (Nyberg et al. 2001). A sys-  
 1230 tematic comparison of locally coexisting populations with  
 1231 non-overlapping spawning times could be therefore a  
 1232 promising approach to achieve mechanistic understanding  
 1233 of the most important factors that make pelagic fish pop-  
 1234 ulations sensitive to global change.

## Conclusions

1235  
 1236 Our review has explored commonalities and differences in  
 1237 pelagic fish species inhabiting either freshwater or estua-  
 1238 rine and marine systems. The potential effects of global  
 1239 change on populations of these fishes will arise from  
 1240 changes in either indirect (trophodynamic) or direct (abi-  
 1241 otic, physiological) factors. The severity of impacts will  
 1242 depend to some extent on whether species have the  
 1243 capacity and speed to adapt to these changes via behav-  
 1244 ioural modification and phenotypic selection.

1245 However, the interplay between genetic differentiation,  
 1246 spatiotemporal distribution, ecological interactions, life



**Fig. 3** Conceptual graphics showing the interplay of processes related to genetic differentiation, spatiotemporal distribution, metabolic specialization, life history and ecology of coregonids (a) and clupeids (b). *Solid arrows* indicate good scientific understanding of

links. *Stippled arrows* indicate links that are suggested to be studied in the next years. Seasonal migrations are not described in coregonids, and hence, this *box* is coloured in *grey*

1247 history and metabolic specialization has differing research  
1248 deficits in clupeids and coregonids (Fig. 3). Whereas in cor-  
1249 egonids, the interaction of thermal windows and bioenergetics  
1250 with habitat choice and vertical migrations is well understood  
1251 (Fig. 3a), these effects are less explored in clupeids. Clupeids  
1252 show large-scale migrations between reproductive and feed-  
1253 ing areas, and individual homing and straying is likely  
1254 important for genetical population differentiation (Fig. 3b). In  
1255 contrast, the spatial and temporal organization of spawning in  
1256 coregonids is not really understood, in particular for the rare  
1257 spring-spawning species.

1258 A central research theme for both groups can be found in  
1259 the interplay between life history and physiological spe-  
1260 cialization, and the resulting genetical differentiation by  
1261 ecological divergence (Fig. 3a, b). Furthermore, the effect  
1262 of host-parasite interactions on local adaptation in this  
1263 context is not understood. It will be important to study  
1264 whether hybrids between species or populations that differ  
1265 in spawning season are fertile, and whether they display  
1266 additive genetic effects with respect to the thermal win-  
1267 dows of their parental populations. This may offer insight  
1268 into the processes that enforce speciation, for example  
1269 through fitness disadvantages of hybrids relative to their  
1270 parents. It cannot be excluded that hybridization between  
1271 metabolically specialized parents is a possible outcome of  
1272 effects of global warming, for example by induction of  
1273 temporal overlap of previously distinct spawning times, or  
1274 habitat temperatures intermediate between those currently  
1275 dominating in the native habitats.

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