Some Atlantic cod *Gadus morhua* in the Baltic Sea visit hypoxic water briefly but often

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Individual behaviour of Atlantic cod *Gadus morhua* in the presence of hypoxic water was measured *in situ* in the vertically stratified Bornholm Basin of the Baltic Sea. Considering all recaptured individuals, the use of hypoxic habitat was comparable to data derived by traditional survey data, but some *G. morhua* had migrated towards the centre of the c.100 m deep basin and spent about a third of their time at oxygen saturation <50%, possibly to forage on zoobenthos. Maximal residence time per visit in such hypoxic water was limited to a few hours, allowing for the digestion of consumed prey items in waters with sufficient dissolved oxygen.

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Hypoxia is a common phenomenon in the Baltic Sea, the Black Sea and the Gulf of St Lawrence (Plante *et al.*, 1998; Tomkiewicz *et al.*, 1998), and hypoxic events are observed with increasing frequencies in lakes and coastal regions (Diaz & Rosenberg, 2008). General knowledge on how hypoxic water volumes limit individual dispersion is crucial to predict the consequences of hypoxic events on the distributions of fish populations in space. So far, this knowledge has been based either on laboratory studies focusing on individual behaviour (Claireaux *et al.*, 1995; Plante *et al.*, 1998; Chabot & Dutil, 1999), or on trawl survey data focusing on the population level distribution limits (D’Amours, 1993; Tomkiewicz *et al.*, 1998; Neuenfeldt & Beyer, 2003).

Here, electronic archival tags were used to measure individual depth experience and measured vertical profiles of oxygen were applied to convert depth data to oxygen saturations. The case study area, the Bornholm Basin (55°20’ N; 16°00’ E), is situated in the Baltic Sea which is the largest estuary in the world. The Baltic Sea consists of several basins with specific vertical profiles of temperature and salinity. A permanent halocline separates low saline surface water from high saline deep water. Oxygen content below the halocline is vertically stratified on the scale of metres.

In 2004 and 2005, 141 and 167 cod *Gadus morhua* L. >450 mm total length (*L*T) were tagged with electronic data-storage tags as detailed in Neuenfeldt *et al.*

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The presented analyses are based on retrieved tag data from 75 recaptured
*G. morhua* (*n* = 41 from 2004 and *n* = 34 from 2005). The tags were of the type
Star-Oddi conductivity temperature depth (CTD) (www.star-oddi.com), and each was
programmed to record pressure, ambient temperature and conductivity once every
12 min. Pressure was measured to an accuracy of ±2 kPa.

Temperature and conductivity measurements were used to locate the *G. morhua*
individuals (Andersen et al., 2007). Thereby, it could be verified that the ones used
later in the analysis did not leave the basin while at large.

Hydrographical data from the Bornholm Basin were used to identify two periods in
2004 and 2005 with constant vertical oxygen gradients in the basin. Oxygen profiles
in the basin are usually quite temporally and spatially homogeneous, with only a slow
decrease in oxygen concentrations below the halocline during the year (Hinrichsen
et al., 2007). In 2004, oxygen gradients were equal in two samplings taken on days
151 and 200 of the year, while in 2005 oxygen saturation did not differ between
two samplings taken on days 150 and 205. Changes of hydrographical conditions on
much smaller time scales, such as hours or days, could occur due to internal wave
motion. Highly spatially and temporally resolved towed CTD measurements did not
detect such high-frequency oscillations below the halocline in the Bornholm Basin
(Stepputtis, 2006).

Individual depth records of the tagged *G. morhua* during the two periods selected
were converted to oxygen ‘experience’ using average vertical oxygen gradients
(Fig. 1). Fish that were periodically subjected to hypoxia (*n* = 10 in 2004 and *n* = 17
in 2005) were identified. The individuals migrated towards the deeper basin centre.
For these 27 fish (total number of data days: 1154), the empirical cumulative density
function (cdf) of time spent at or below oxygen saturation was calculated. In order to
allow for a comparison to the complete tagged population, the empirical cumulative
density function of time spent at or below oxygen saturation was calculated for all
recaptured *G. morhua*, (total number of data days: 2185). Maximum residence time
was defined as the 99% percentile of residence time at a given maximal oxygen
saturation. A value of 10 h at 30% oxygen saturation, for example, indicates that
99% of the residence times *G. morhua* stayed at oxygen saturation between 0 and
30% were ≤10 h.

The 27 fish that had moved towards the basin centre experienced oxygen
saturations as low as 10%, and spent half of their time at oxygen saturation <70%,
and a third of their total time at oxygen saturation <50% (Fig. 1). Seven per cent
of their total time was spent at oxygen saturation ≤20% (Fig. 1), an approximate
oxygen saturation level that killed 50% of *G. morhua* over 96 h under laboratory
conditions (accurately 21-2% saturation level, Plante et al., 1998). This means that
out of 1154 individual *G. morhua* days with recorded depth data, 80-8 days were
spent at a depth corresponding to oxygen saturation ≤20%. Assuming that all fish
in this group visited hypoxic conditions at the same intensity, an average *G. morhua*
would hence have experienced 3 days of oxygen saturation ≤20% during the on
average 42-7 days of recording in 2004 and 2005.

A slightly lower number of data days was gathered from *G. morhua* that did not
migrate towards the basin centre (1031 days). Combining the cdf for the migratory
and the coastal *G. morhua* allows for an assessment of the overall use of hypoxic
waters by the tagged population. Considering the complete recaptured population,
the fish spent 30% of their time at oxygen saturation <70%, and 18% of their time
at oxygen saturation <50%. It is, however, of note that the two groups frequented different areas of the basin.

Focusing on the group of *G. morhua* that migrated towards the basin centre and encountered hypoxic waters, the total residence time per fish was not accumulated during one extended visit to hypoxic water. Instead, average residence time per fish per observed visit at oxygen saturation <20% was much shorter (1.5 h, Fig. 1). The maximal residence time was 12 h (Fig. 1), which is still short as compared to 72 h (3 days). Hence, excursions down into hypoxic water were undertaken as short vertical migrations, on average about once per day.

The *G. morhua* probably moved into the hypoxic water to forage. *Gadus morhua* have under laboratory conditions been observed to move into hypoxia (O₂ ≤ 16%) for a couple of minutes when food was offered (Claireaux et al., 1995). Both observations of sprat *Sprattus sprattus* L. concentrations at very low oxygen levels down to c. 10% saturation (Stepputis, 2006; Schaber et al., 2009) and the presence of benthic food in the stomachs of pelagic *G. morhua* during spawning season (Neuenfeldt & Beyer, 2003) indicate that *G. morhua* will dive into hypoxic water in order to forage. Deep-burrowing prey species, emerging from the sediment when oxygen is depleted, are relatively easily to access for predatory *G. morhua* (Jørgensen, 1980). This might be the reason for observed high consumption by demersal fishes of deep-burrowing species during hypoxic periods (Pihl, 1994), and would further support that *G. morhua* move into hypoxic water because of easily accessible food.

In this special case, the appearance of hypoxia might therefore not reduce *G. morhua* growth as observed under laboratory conditions (Chabot & Dutil, 1999), but even increase it. The individuals use the high prey availability in the hypoxic region, and digest the food in the normoxic region.

Focusing exclusively on the threshold nature of hypoxia for the distribution of marine species, the usage of data-storage tags did not reveal new insights. Compared
to traditional sampling methods such as trawl surveys (D’Amours, 1993; Chabot, 2004), surveys have furthermore the advantage, that a greater proportion of the population can be sampled.

In contrast to scientific surveys, however, the application of electronic data-storage tags together with hydrographic data allowed individual residence periods to be monitored continuously over the full range of available oxygen conditions. Such data enable the identification of behavioural mechanisms beyond avoidance.

By actively using the hypoxic part of their habitat to forage during short periods that may not affect consumption rates, \textit{G. morhua} could possibly increase growth. Residence in hypoxia is probably not a memory less behaviour. Future assessments of the oxygen debt and energy budget under residence in such hostile environmental conditions will substantially support the development of process-based knowledge, combining dispersion and growth in environmental limiting conditions.

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