



Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry



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The potential for populations to undergo adaptive evolution depends on individual variation in traits under selection and how multiple traits are correlated. While fitness relates to the performance of animals in the wild, most of the research on evolutionary potential of behavioural traits has used captive or mesocosm settings, especially with aquatic organisms. We investigated the individual level consistency (personalities) and correlations (behavioural syndromes) of fitness-related behavioural traits displayed by a harvested marine fish in the natural environment, and the potential of such individual level behaviour to constrain adaptive evolution. For this, we acoustically tracked 303 individuals of Atlantic cod, *Gadus morhua*, over a period of 3 years from two populations in southern Norway. We then estimated repeatability and correlations between four behavioural traits: diel vertical migration, activity, home range and dispersal. Average autonomy was estimated as a measure of the potential of the observed behavioural syndromes to constrain evolution. We found a moderate to high individual consistency in all behavioural traits (mean repeatability 0.41, range 0.22–0.66) suggesting that they reflect fish personalities. Also, behavioural traits were structured into behavioural syndromes, where one population displayed a more integrated behavioural syndrome (all the four traits correlated) than the other (only home range and dispersal correlated). In both populations, the magnitude of these behavioural syndromes could potentially constrain evolution, as revealed by average autonomy values significantly below 1. Our study provides strong empirical support to the idea that natural and human-induced selection on behavioural traits can indeed drive adaptive evolution, and, further, that such evolutionary responses may be constrained by the correlational structure among multiple traits.

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A rush of recent research has documented the importance of intraspecific trait variation to ecological and evolutionary processes (Bolnick et al., 2011; Wolf & Weissing, 2012). Comparatively, the ecological and evolutionary consequences of individual variation in behaviour have so far received little attention (Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012). This is surprising given that behaviour has a key role in mediating the interactions of individuals with the surrounding environment (Wolf & Weissing, 2012). For instance, behavioural traits can, under many circumstances, determine fitness to an extent the same as or greater than life history characteristics by being the traits directly under

selection (Kinnison, Hendry, & Stockwell, 2007; Stockwell, Hendry, & Kinnison, 2003; Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008). Although changes in selection regimes will often be a natural process, humans are also reshaping the selective environments around the globe at unprecedented rates (Stockwell et al., 2003). For instance, human harvesting may pose strong selection on the target population by removing individuals with particular behavioural types (e.g. more active or bolder; Alós, Palmer, & Arlinghaus, 2012; Biro & Post, 2008).

Whether species will be able to adapt in response to new agents of selection will be determined by the strength of the selection and heritability of the traits (Stockwell et al., 2003). When confronted with a new selective regime, standing genetic variation in behavioural traits can fuel rapid evolutionary responses (Barrett & Schluter, 2008; Wolf & Weissing, 2012). By speeding up evolution, individual level variation in behaviour (i.e. animal personality)

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therefore affects the interplay between ecology and evolution, with both processes proceeding at contemporary timescales (i.e. contemporary evolution; Stockwell et al., 2003).

Estimating the heritability of behavioural traits ideally requires information on the pedigree of a population (Brommer, 2014). However, pedigrees are rarely available for wild animals in their natural environment. In these cases, repeatability estimates hold promise as a tool for making evolutionary inferences (Dochtermann, 2011; Dochtermann, Schwab, & Sih, 2015). If traits are repeatable, a fundamental next step is to identify whether or not they are correlated at the between-individual level forming what has been termed behavioural syndromes (Dingemanse & Dochtermann, 2012). Although it remains unsolved how stable such correlations are at the genetic level in the long term, the effect of behavioural syndromes can still be manifested in the short term through fitness consequences of changes in multiple traits (Dochtermann & Dingemanse, 2013; Wolf & Weissing, 2012). Although behavioural syndromes may in some cases promote the capacity of a population to evolve solutions to novel ecological problems, they are often considered to constrain or retard adaptive evolution by preventing a fitness peak being achieved on an adaptive landscape because the correlated traits cannot evolve independently (Dochtermann & Dingemanse, 2013; Sih et al., 2004; Wolf & Weissing, 2012).

Behavioural traits are typically measured over short time periods in the laboratory, whereas estimates of long-term consistency and correlations in the wild are scarce (e.g. Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; Harrison et al., 2014), especially in marine systems (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). This is unfortunate, because the covariance components of traits estimated in captivity may not adequately reflect the covariances of traits measured in the wild (Bell, Hankison, & Laskowski, 2009; Niemelä & Dingemanse, 2014). Conducting behavioural studies in nature where selection and ultimately evolution act is, therefore, vital (Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Quantifying behavioural consistency in wild aquatic environments, however, is intrinsically difficult because the animals cannot readily be observed and each individual must be assayed multiple times for the same trait, which is a logistic challenge. Fortunately, recent refinement of tracking technologies allows behavioural information from aquatic animals to be gathered over large temporal and spatial scales (Hussey et al., 2015). Although a typical feature of tracking data sets is the existence of substantial individual differences in spatial behaviour (e.g. Moland et al., 2011), the analysis of this variability has largely focused on understanding the role of external cues or intrinsic factors such as size or sex; the potential for such data sets to provide information about consistency and covariation in behavioural traits remains largely unexplored (Liedvogel, Chapman, Muheim, & Åkesson, 2013).

Coastal populations of Atlantic cod, *Gadus morhua*, are well suited for investigating consistency of behavioural traits in the wild, because these fish are typically very sedentary and can be monitored for long periods of time (e.g. Freitas, Olsen, Moland, Ciannelli, & Knutsen, 2015; Olsen, Heupel, Simpfendorfer, & Moland, 2012). In southern Norway, coastal cod are genetically structured into local populations on the scale of fjords (tens of kilometres), with a role for local topography in shaping population structure and a strong potential for local adaptations (Jorde, Knutsen, Espeland, & Stenseth, 2007; Rogers, Olsen, Knutsen, & Stenseth, 2014). We investigated the repeatability and correlation of behavioural traits of coastal cod from two neighbouring fjord populations in southern Norway. During more than 3 years, a total of 303 individuals were acoustically tracked in their natural environment. We selected four behavioural traits that describe the spatial ecology of many aquatic animals and have the potential to affect the fitness of the

individuals. Two of the selected traits, diel vertical migration and activity, can determine vulnerability to fishing by increasing the chances of finding and being trapped in passive gears (Alós et al., 2012; Olsen et al., 2012). The other two traits analysed, home range size and dispersal, may affect fitness in scenarios of spatial protection by determining the time spent beyond reserve boundaries, i.e. the time at risk (Baskett & Barnett, 2015; Parsons, Morrison, & Slater, 2010; Villegas-Ríos, Moland, & Olsen, 2016).

We hypothesized that (1) a significant proportion of the phenotypic variance in cod behavioural traits is explained by consistent between-individual differences defined as personality traits, (2) these traits are correlated at the between-individual level forming behavioural syndromes and (3) covariation between behavioural traits is important enough to constrain evolution. By analysing the same traits in two different populations during the same period, we were able to investigate the extent to which the observed patterns of consistency and correlations between traits vary between environments (fjords). Broadly, our study provides empirical field-based inference on the potential of behavioural traits to evolve in response to natural- and human-induced selection in aquatic environments.

METHODS

Ethical Note

This research was carried out in line with the Norwegian Animal Research Review Panel (Forsøksdyrutvalget) under permit number 6037, and it adheres to the ASAB/ABS Guidelines for the use of animals in research. Details on the capture, handling and tagging process are provided below.

Study Sites and Telemetry Arrays

Behavioural traits were quantified for wild coastal cod from two populations in Skagerrak, southern Norway, separated by about

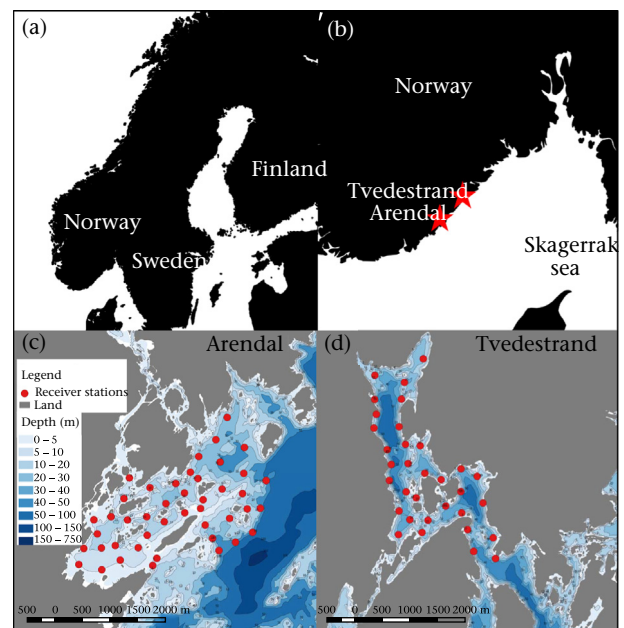


Figure 1. Map of the study area and telemetry arrays. (a) The study was conducted in the south of Norway in two sites connected to the Skagerrak Sea: (b) Arendal coast and Tvedestrand fjord. Telemetry arrays consisted of 44 receiver stations in (c) Arendal and 33 in (d) Tvedestrand.

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