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ORIGINAL PAPER

Comparative population genetics of seven notothenioid fish species reveals high levels of gene flow along ocean currents in the southern Scotia Arc, Antarctica

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Abstract The Antarctic fish fauna is characterized by high endemism and low species diversity with one perciform suborder, the Notothenioidei, dominating the whole species assemblage on the shelves and slopes. Notothenioids diversified in situ through adaptive radiation and show a variety of life history strategies as adults ranging from benthic to pelagic modes. Their larval development is unusually long, lasting from a few months to more than a year, and generally includes a pelagic larval stage. Therefore, the advection of eggs and larvae with ocean currents is a key factor modulating population connectivity. Here, we compare the genetic population structures and gene flow of seven ecologically distinct notothenioid species of the southern Scotia Arc based on nuclear microsatellites and mitochondrial DNA sequences (D-loop/cytochrome *b*). The seven species belong to the families Nototheniidae (*Gobionotothen gibberifrons*, *Lepidonotothen squamifrons*, *Trematomus eulepidotus*, *T. newnesi*) and Channichthyidae (*Chaenocephalus aceratus*, *Champsocephalus gunnari*, *Chionodraco rastrospinosus*). Our results show low-population differentiation and high gene flow for all investigated species independent of their adult life history strategies. In addition, gene flow is primarily in congruence with the prevailing ocean current system, highlighting the role of larval dispersal in population structuring of notothenioids.

Keywords Notothenioids · Adaptive radiation · Scotia Arc · Dispersal · Isolation-with-migration · Population genetics

Introduction

The Southern Ocean surrounding the Antarctic continent is a unique marine environment and its fish fauna is characterized by a high degree of endemism at low species diversity (Andriashev 1987; Eastman 1993, 2005). The northern boundary of the Southern Ocean is delimited by the Antarctic Convergence at about 50–60°S, which is marked by a sharp decrease of surface temperature from north to south and constitutes a thermal barrier for many marine organisms existing since approximately 22–25 My (Dayton et al. 1994; Eastman and McCune 2000). Besides its thermal isolation, the formation of deep circum-polar currents like the Antarctic Circumpolar Current (ACC) as well as large distances and deep ocean basins between the Antarctic continental shelf and those of adjacent continents form additional oceanographic, geographic and bathymetric barriers to migration and dispersal. The Antarctic ichthyofauna as known today consists of 322 species from 50 families, with about 88% being endemic to the waters south of the Antarctic Convergence. A single group of fish, the perciform suborder Notothenioidei, dominates the species assemblage on the shelves and slopes (Andriashev 1987; Eastman 2005).

Notothenioids consist of 131 species in 8 families, with 104 species out of 5 of these families being endemic to the Antarctic region, where they constitute up to 77% of

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species diversity and 91% of biomass on the shelves and slopes of the continent and nearby islands (Eastman 2005). Together with members of the families Zoarcidae (24 species) and Liparidae (70 species), they comprise 88% of the Antarctic fish fauna (Eastman and McCune 2000). But unlike the latter two families that probably invaded the area from North Pacific waters, notothenioids diversified in situ in the course of an adaptive radiation (Eastman 1993; Clarke and Johnston 1996; Eastman and McCune 2000; Matschiner et al. 2011). This radiation is thought to have been triggered by the acquisition of antifreeze glycoproteins (AFGPs) that keep body fluids from freezing in the ice-laden waters of Antarctica (Cheng 1998; Matschiner et al. 2011). While the cooling of Antarctic waters as well as repeated expansions and retreats of the Antarctic ice sheet forced most Antarctic species of the Oligocene to either shift their distribution northwards or into deeper waters, or otherwise led to their extinction (Briggs 2003; Barnes and Conlan 2007), notothenioids radiated in the absence of competitors and filled vacant ecological niches (Eastman 1991). Although about one-half of today's species show a demersal lifestyle (as is also presumed for their ancestors), the notothenioid radiation is largely based on diversification related to niches in the water column (Eastman 1993). Since notothenioids lack a swim bladder, buoyancy for pelagization is gained through extended lipid depositions and reduced ossification (Eastman 1993), resulting in a variety of epibenthic, semipelagic, cryopelagic, and pelagic life strategies. Adaptive radiations in the marine realm are rare compared to those known from freshwater systems like, for example, cichlid fishes in the Great Lakes of East Africa (Seehausen 2006; Salzburger 2009; Matschiner et al. 2010) or are camouflaged by subsequent dispersal in the course of evolution. The notothenioids therefore constitute a prime example for a marine adaptive radiation, making their ecological and morphological diversification a highly interesting target for evolutionary studies (Eastman 2000).

In contrast to the variety of adult life history strategies, the early larval development in notothenioids is always pelagic. Depending on the species and locality, the larval stage may be completed within 2 months after hatching or last more than 1 year (Kellermann 1986, 1989; North 2001). During this stage, strong currents like the clockwise ACC (Westwind Drift) or the counterclockwise Eastwind Drift along the Antarctic continent are likely to modulate larval dispersal away from the shelves into the open ocean. This may cause substantial losses to spawning populations and can lead to source–sink relationships by transporting larvae downstream toward distant shelf habitats. As White (1998) pointed out, the prolonged pelagic early life history strategy in notothenioids is at odds with a successful larval survival strategy. However, ichthyoplankton studies have shown that larval abundances for demersal species are surprisingly high on the shelf areas and decrease with increasing distance to the coast, despite the fact that their distributions are generally influenced by bathymetry, hydrography, and seasonal events (Loeb et al. 1993; White 1998). Local retention mechanisms, such as gyres formed behind islands or shelf-break frontal systems limit offshore transport of larvae (White 1998) and should increase genetic heterogeneity between populations of different shelves, thereby fostering speciation.

Population genetic studies in notothenioids provide evidence that the oceanography of the Southern Ocean indeed has large influence on the genetic structure of populations. Populations of species with circumpolar distributions as, for example, the pelagic Antarctic toothfish *Dissostichus mawsoni* and the more sedentary benthopelagic Patagonian toothfish *D. eleginoides* are not significantly differentiated over large parts of their distribution range (Smith and Gaffney 2005; Rogers et al. 2006). However, these results do not imply complete absence of genetic heterogeneity, as other genetic markers were able to resolve differentiations on varying geographic scales (Parker et al. 2002; Shaw et al. 2004; Kuhn and Gaffney 2008). Populations connected along currents like the ACC are often found to be more closely related than those located in proximity but separated across frontal systems like, for example, the Polar Front (Shaw et al. 2004; Rogers et al. 2006). Even strictly benthic species like the humped rockcod *Gobionotothen gibberifrons* show no signs of differentiation among populations separated geographically by nearly 2,000 km and bathymetrically by deep basins (Matschiner et al. 2009). By combining oceanographic data with population genetic signatures, Matschiner et al. (2009) showed that dispersal of pelagic larvae in *G. gibberifrons* is most probably the major means of gene flow in this otherwise benthic species. The contribution of larval dispersal to population structure and in the long term on species' biogeography is still lively debated not only in notothenioids, but also in fish from warmer waters with distinctly shorter pelagic early life stages (e.g. Taylor and Hellberg 2003; Bay et al. 2006; Cowen and Sponaugle 2009). In particular, it is unclear what influence a prolonged pelagic early life stage and the existence of strong currents (which together should result in high levels of gene flow among populations) had on the adaptive radiation in notothenioids.

In this study, we compare the genetic signatures derived from microsatellites and mitochondrial (mt) DNA sequences of seven notothenioid species with different life history strategies and larval durations inhabiting the southern Scotia Arc (Table 1). It is the first time that the genetic population structures based on two types of genetic markers are compared between multiple notothenioid species. We also included data obtained from drifting buoys to infer the

Table 1 Distribution area and selected life history characteristics for all seven study species

Family Species	Distribution range	Depths range [m]	Adult habit	Eggs	Spawning time	Hatching time	Abs. fecund.	Gen. time (years)
Channichthyidae								
C. aceratus	Scotia Arc region, Bouvet Is[a]	5–770[b]	Benthic[c]	Bottom, guarded[d]	May–Jun[e]	Aug–Nov[e,f]	3,082–22,626[c,g]	6–8[h]
C. gunnari	Scotia Arc region, Bouvet Is, Kerguelen Is, Heard Is[a]	0–700[a]	Bentho-pelagic[c]	Bentho-pelagic or pelagic[c], scattered	Jun–Jul[e]	Jan–Mar[e,i]	1,294–31,045[j,k]	3[h]
C. rastrospinosus	South Orkney Is, South Shetland Is, Antarctic Peninsula[a]	0–1,000[b]	Bentho-pelagic[b]	Demersal[c], scattered	Mar–May[e,l]	Sep–Oct[i,m]	1,464–5,136[e]	4–8[n,o]
Nototheniidae								
G. gibberifrons	Scotia Arc region[p]	5–750[p]	Benthic[a,f]	Demersal[q], scattered	Aug–Sep[e]	Nov–?[e]	21,699–143,620[e]	6–8[h]
L. squamifrons	Sub-Antarctic Islands, intervening seamounts of the Indian Ocean sector, Scotia Arc region, Bouvet Is[p,r]	5–670[s,t]	Benthic[a,f]	Demersal[q], scattered	Feb–Mar[l,u]	Apr–Jun[v]	38,000–280,000[w,x]	7–9[v]
T. eulepidotus	Circum-Antarctic: nearshore and continental shelf and nearby islands[p]	70–550[p]	Bentho-pelagic[a,b]	Substrate[y], non-guarded	Apr[l]	Sep[y]	1,400–12,854[h,z]	7[y]
T. newnesi	Circum-Antarctic: shallow shelf waters of the continent and adjacent islands[p]	0–400[aa]	Bentho-cryo-pelagic[bb,cc]	?	Mar–May[dd,ee]	Sep–Nov[h,cc]	2,300–12,200[dd]	?

Spawning and hatching times are for the region of South Shetland Islands and the Antarctic Peninsula

[a] Iwami and Kock (1990), [b] Hureau (1985), [c] Permitin (1973), [d] Detrich et al. (2005), [e] Kock (1989), [f] Ślósarczyk (1987), [g] Lisovenko and Sil'yanova (1980), [h] Kock and Kellermann (1991), [i] Kellermann (1989), [j] Kock 1981, [k] Lisovenko and Zakharov (1988), [l] Kock et al. (2001), [m] Kock and Jones (2005), [n] Kock (2005b), [o] La Mesa and Ashford (2008a), [p] DeWitt et al. (1990), [q] Permitin and Sil'yanova (1971), [r] Schneppenheim et al. (1994), [s] Duhamel (1981), [t] Ekau (1990), [u] Kellermann (1986), [v] Duhamel and Ozouf-Costaz (1985), [w] Lisovenko and Sil'yanova (1979), [x] Kock (1992), [y] Ekau (1989), [z] Ekau (1991), [aa] Tiedtke and Kock (1989), [bb] Andriashev (1987), [cc] Radtke et al. (1989), [dd] Shust (1987), [ee] Jones and Kock (2006)

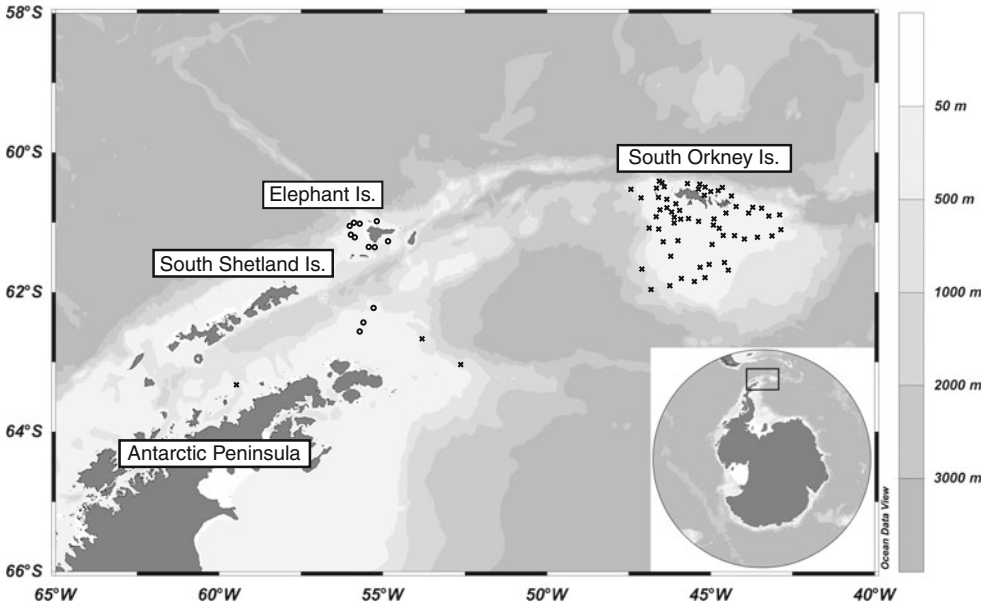

Fig. 1 Study area and sampling localities in the southern Scotia Arc, Antarctica. *Open circles* = stations sampled during ANT-XXIII/8 2006, *crosses* = stations sampled during US AMLR 2009 finfish survey

influence of larval dispersal with oceanic currents on gene flow. Our study area is the southern Scotia Arc, consisting of the tip of the Antarctic Peninsula (AP), South Shetland Islands (SSh) including Elephant Island (EI) located about 200 km north of the Peninsula and the South Orkney Islands (SO) approximately 420 km further east (Fig. 1). The shelves of the AP and SSh/EI are separated by trenches of more than 500 m depth, whereas the SO shelf is separated by depths of 2,000–3,000 m. This region of the Seasonal Pack-Ice Zone, which is ice-free during the austral summer, is largely influenced by two water regimes: the ACC flowing eastward through the Scotia Sea in the north and water originating from the Weddell Sea in the south (Whitworth et al. 1994).

The species investigated in this study comprise the three channichthyids *Chaenocephalus aceratus*, *Champsocephalus gunnari*, and *Chionodraco rastrospinosus* as well as the four notothenioids *G. gibberifrons*, *Lepidonotothen squamifrons*, *Trematomus eulepidotus*, and *T. newnesi*, which are all among the most abundant species in the southern Scotia Arc. Their life histories differ in a variety of traits (Table 1): *C. aceratus*, *G. gibberifrons*, and *L. squamifrons* are benthic species of which the two former ones spend most of their time resting on the bottom (Fanta et al. 1994; Kock and Jones 2005). *C. gunnari*, *C. rastrospinosus*, and *T. eulepidotus* show a benthopelagic lifestyle preying for food in the water column (Rutschmann et al. 2011). Vertical migrations between near bottom layers during the day and sub-surface waters during the night are known from several notothenioids including *C. gunnari* (Kock and Everson 1997). *T. newnesi* shows a remarkable feeding plasticity and is considered a bentho-cryo-pelagic species (La Mesa et al. 2000). It is generally benthivorous, but carries out vertical migrations during summer feeding on pelagic organisms. In winter, when there is sea ice cover, *T. newnesi* switches to a cryo-pelagic mode and feeds on organisms under the ice (Daniels 1982; Casaux et al. 1990; La Mesa et al. 2000).

The aim of this study is to investigate the role of prolonged larval stages on the genetic population structures of notothenioids. Dispersing larvae should result in high similarities between geographically separated populations even in those species that show a more sedentary habit as adults. We hypothesize that a high connectivity between populations is a general characteristic of notothenioids when hydrographic currents connect geographically separated populations.

Methods

Sampling

The specimens analyzed in this study were collected during expedition ANT-XXIII/8 aboard RV Polarstern in December 2005-January 2006 and U.S. AMLR (United States Antarctic Marine Living Resources) finfish survey in February–March 2009 aboard RV Yuzhmorgeologiya. Sampling sites were located on the shelves at the tip of the AP, EI (the most easterly island of the SSh), and SO to their east (Fig. 1). Muscle tissue of the specimens was stored in 95% ethanol. DNA was extracted using two different protocols depending on the cruise. All 2005–2006 samples were extracted with the BioSprint 96 workstation (QIAGEN) following the manufacturer's protocol, whereas DNA from the AMLR 2009 samples was extracted by incubating muscle

tissue in 300 µl 5%-Chelex solution containing 12 µl Proteinase K (20 mg/ml) for 3 h at 55°C, followed by a denaturation step of 25 min at 98°C in a thermomixer.

MtDNA sequencing and data analysis

Depending on the amplification success, mitochondrial gene sequences were either generated from the control region/D-loop (*C. aceratus*, *C. gunnari*, *C. rastrospinosus*, and *G. gibberifrons*) or cytochrome *b* (cyt *b*; *L. squamifrons*, *T. eulepidotus*, and *T. newnesi*). Partial D-loop or cyt *b* were amplified with the primers LPR-02 and HDL2 (Derome et al. 2002) or NotCytbF and H15915n (Matschiner et al. 2011), respectively. For amplification of the D-loop region, 2 µl template DNA was mixed with 7.5 µl Taq PCR Master Mix (QIAGEN), 0.5 µl of each 10 µM primer, 1 µl bovine serum albumin, and 14.5 µl sterile water. A simplified hot start at 94°C for 2 min initiated the PCR profile followed by 35 cycles of 94°C for 30 s, 52°C for 30 s, and 72°C for 90 s. Thermocycling finished with a final elongation step at 72°C for 7 min. Cytochrome *b* sequences were amplified using Phusion polymerase (Finnzymes) following the manufacturers manual at 57°C annealing temperature. PCR products were purified by adding 2 µl ExoSAP-IT (USB Corporation) to 5 µl PCR product following the manufacturer's instructions.

Sequencing PCR with forward primers was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). After purification with BigDye XTerminator (Applied Biosystems), sequencing products were run on an AB3130*xl* Genetic Analyzer (Applied Biosystems). Sequences were automatically aligned with CodonCode Aligner (CodonCode Corp.), inspected by eye, and corrected manually if necessary.

Basic sequence properties as well as intraspecific sequence polymorphisms measured as nucleotide diversity (π) and haplotype diversity (h) were examined with DnaSP 5.10 (Librado and Rozas 2009). Population structure among sampling localities was assessed by analysis of molecular variance (AMOVA) based on traditional *F*-statistics and calculated with 16,000 permutations as implemented in Arelquin 3.5 (Excoffier and Lischer 2010).

Phylogenetic trees were inferred with the Maximum Likelihood (ML) method implemented in PAUP* 4.0a112 (Swofford 2003), whereby models of sequence evolution were selected according to BIC (Posada 2008). On the basis of these phylogenies, haplotype genealogies were constructed following the method described in Salzburger et al. (2011).

The statistical power of both mtDNA and microsatellites to detect significant genetic differentiation between populations was tested with POWSIM 4.0 (Ryman and Palm 2006) using both the chi-squared test and Fisher's exact test. Various levels of differentiation (measured as F_{ST} in the range from 0.001 to 0.08) were tested by combining different effective population sizes (N_e) and times since divergence (t). In addition, POWSIM allows calculating the α error (type I error), which is the probability of rejecting the null hypothesis of genetic homogeneity although it was true by drawing the alleles directly from the base population ($t = 0$).

Microsatellite genotyping and data analysis

In addition to mtDNA sequences, we included data of twelve previously published microsatellites in our analyses. Microsatellites Cr15, Cr38, Cr127, Cr236, Cr259 were originally isolated from *Chionodraco rastrospinosus* (Papetti et al. 2006), Trne20, Trne35, Trne37, Trne53, Trne55, Trne66 from *Trematomus newnesi* (Van Houdt et al. 2006), and Ca26 from *Chaenocephalus aceratus* (Susana et al. 2007). Marker sets for each species were composed of 8–10 microsatellites, depending on the amplification success (Online Resource 1).

All amplification reactions contained 5 µl Multiplex Master Mix (QIAGEN), 0.2 µl of each 10 µM primer, 0.8 µl template DNA and water added to a final volume of 10 µl. All reactions contained primers for up to 3 microsatellites of which the forward primers were fluorescently labeled. The PCR profile was 95°C for 15 min followed by 35 cycles of 94°C for 30 s, 59°C for 90 s, 72°C for 90 s, and final elongation at 72°C for 10 min. Fragment lengths were determined with GeneScan LIZ500 size standard (Applied Biosystems) on an AB3130xl Genetic Analyzer (Applied Biosystems) and scored with GeneMapper 4.0 (Applied Biosystems).

Alleles were automatically binned with Tandem (Matschiner and Salzburger 2009) and subsequently converted with Convert (Glaubitz 2004). We used a 3D factorial correspondence analysis as implemented in Genetix (Belkhir et al. 2001) to visualize outliers in the data. Suspicious individuals with potential errors in the data were corrected, re-genotyped, or otherwise completely removed from the data set.

Microsatellites were tested for the presence of null alleles, stuttering and large allele dropout with Micro-Checker 2.2.3 (Van Oosterhout et al. 2004). Allele size ranges, Hardy–Weinberg-Equilibrium (HWE) per population and species as well as genotypic linkage disequilibrium between loci were examined in Genepop 4.0.10 (Raymond and Rousset 1995).

The number of alleles per sample and locus were calculated with FSTAT (Goudet 1995, 2001) using the implemented rarefaction method to account for differences in sample sizes.

Population structure was assessed performing an AMOVA based on traditional *F*-statistics as implemented in Arlequin 3.5 (Excoffier and Lischer 2010). To account for biases attributed to null alleles present in the data, F_{ST} values were also calculated excluding null alleles with FreeNA (Chapuis and Estoup 2007). Arlequin was further used to test loci for HWE in each population. Molecular diversities were measured as mean number of pairwise differences and average gene diversity. The Garza-Williamson index was calculated as indicator of recent demographic history. This statistic is sensitive to population size reductions since a recent bottleneck usually reduces the number of alleles more than the allele size range hence leaving "vacant" positions in between. The index is supposed to be very small in populations having experienced a recent bottleneck and close to one in stationary populations (Garza and Williamson 2001). In a similar approach populations were tested for a recent reduction in effective population size with Bottleneck 1.2.02 (Piry et al. 1999) using the two-phase model (TPM) of mutation with 10% infinite allele model (IAM) and 90% single step mutation model (SMM) with a variance of 15% and 1,000 iterations. Significance was tested with the Wilcoxon signed-rank test. In addition, we used the mode-shift indicator as qualitative descriptor of allele frequency distribution. A normal L shaped distribution indicates populations in mutation-drift equilibrium whereas a shifted mode is a sign for recent bottlenecks. We considered that a population truly underwent a bottleneck if this was indicated by all three measurements (low Garza-Williamson index, significant Wilcoxon signed-rank test and mode shift).

To further analyze the structure of populations and to identify clusters of individuals, we used a Bayesian approach based on the genotypes of microsatellites as implemented in Structure 2.3.1 (Pritchard et al. 2000). For every data set we ran simulations for up to 6 clusters (k) with 20 iterations each. The parameters were set to 10,000 steps of burn-in period and 100,000 MCMC replications thereafter. The admixture model was used as we expected a weak population structure as often encountered in marine fishes with long larval phases (and indicated by our calculated F_{ST} values). Alpha was inferred from an initial value of 1.0 and correlated allele frequencies with lambda set to 1.0. In a second approach we ran the program with the same settings but incorporated a priori information about the sampling sites to help with clustering. We followed the method of Evanno et al. (2005) to calculate Δk as indicator of the most likely number of clusters. The power of microsatellites to detect significant population structure was tested in the same way as the mtDNA sequences using POWSIM 4.0 (Ryman and Palm 2006) but in the F_{ST} range of 0.001–0.01.

Isolation-with-migration analyses

The directionality and extent of gene flow between AP/EI and SO populations was examined for the combined data set of mtDNA sequences and nuclear microsatellites with the isolation-with-migration (IM) model as implemented in IMa2 (Hej and Nielsen 2007). The Hasegawa-Kishino-Yano (HKY) model of sequence evolution was applied to mitochondrial sequences, and a stepwise mutation model (SMM) was assumed for all microsatellite loci. Inheritance scalars of 0.25 and 1 were assigned to mtDNA and microsatellite loci, respectively. Appropriate prior parameter ranges were determined in a series of initial runs. We chose wide population size parameter ranges Θ_1, Θ_2, Θ_A ε (0,500], a divergence time prior $t \in (0,10]$, and exponential migration rate priors m_1, m_2 with distribution means of 5.0. Each run included 80 Metropolis-coupled Markov chains. Geometric heating scheme parameters were chosen to optimize chain swap rates, and set to ha = 0.97 and hb = 0.86. Per population comparison, ten replicate runs were conducted for 4.5 million generations, discarding the first 500 000 generations as burn-in. The consistent genealogies of run replicates were jointly analyzed in IMa2's "Load Trees"-mode. The migration rates per year (M) were calculated from the resulting parameters $M = \Theta \times m/2$ under consideration of the species' generation times.

Drifter analysis

In order to compare directionality of gene flow and ocean currents, we also analyzed trajectories of satellite-tracked drifting buoys (hereafter called drifters) of the Global Drifter Program (Lumpkin and Pazos 2007), following established protocols (Matschiner et al. 2009). Interpolated drifter data was downloaded from http://www.aoml.noaa.gov/phod/dac/gdp.html for all drifters passing the AP/SO region (55–65°S, 40–60°W) between 15 February 1979 and 31 December 2009. Three polygons were mathematically defined to encompass the AP, EI, and SO shelf areas at 500 m depth. Polygon vertices were 65.0°S, 60.0°W; 65.0°S, 54.5°W; 63.9°S, 54.1°W; 63.3°S, 52.3°W; 62.2°S, 54.3°W; 62.1°S, 55.4°W; and 63.3°S, 60°W for the AP, 62.7°S, 60°W; 61.4°S, 54.1°W; 61.1°S, 53.9°W; 60.8°S, 55.7°W; and 61.9°S, 60.0°W for EI, and 62.3°S, 44.8°W; 61.5°S, 44.0°W; 61.2°S, 42.4°W; 60.8°S, 42.8°W; 60.3°S, 46.6°W; 60.5°S, 47.3°W; and 61.6°S, 46.9°W for SO. Trajectories of drifters passing these polygons were plotted for 90 days, starting with the day of departure from one of the polygons (Fig. 2).

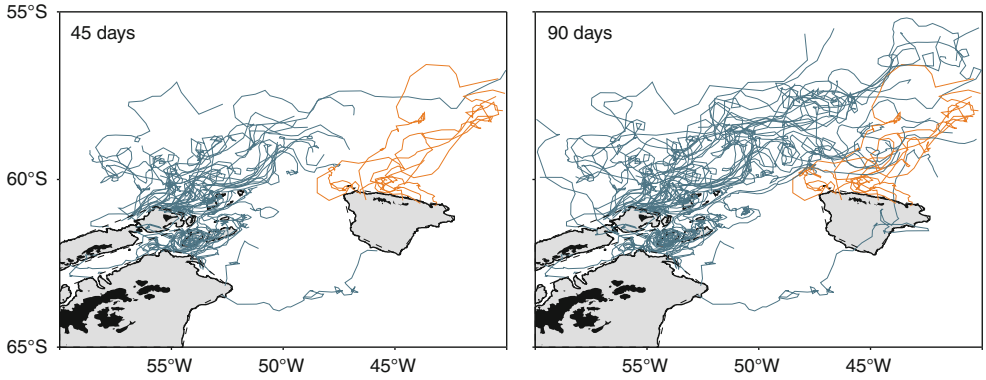

Fig. 2 Trajectories of surface drifters 45 and 90 days after leaving the shelves (500 m isobath *contour line*) of South Shetland/Antarctic Peninsula (*blue*) and South Orkney Islands (*yellow*)

Results

mtDNA: genetic diversity and demographic history

The number of individuals successfully sequenced varied between species and ranged from 49 (*L. squamifrons*) to 194 (*G. gibberifrons*; Online Resource 2). The D-loop region could be amplified in 4 out of 7 species (*C. aceratus*, *C. gunnari*, *C. rastrospinosus* and *G. gibberifrons*). For the remaining three species *L. squamifrons*, *T. eulepidotus* and *T. newnesi* amplification of the D-loop region consistently failed. Therefore, we amplified a part of the mt cyt *b* gene as an alternative population genetic marker. Although we are aware that the use of two mtDNA markers is not optimal and hinders a direct comparison between data sets without restrictions, we found both markers to resolve the population genetic structures in a similar fashion. All sequences generated were submitted to GenBank (Accession nos JN241690-JN241831) and a list of haplotypes per shelf area can be found in Online Resource 3. Although a clear relationship between sample size or sequence length and the number of haplotypes could generally be expected, no such trend was found ($R^2 = 0.06$ and $R^2 = 0.18$, respectively). Similarly, the genetic diversities varied between species, but irrespective of the locus or phylogenetic relationship. Remarkably, the three high-Antarctic species *C. rastrospinosus*, *T. eulepidotus* and *T. newnesi* had the highest nucleotide diversities (each > 0.004) and a similar pattern arose from the haplotype diversities. On the population level, most samples from the AP region had higher diversities than SO samples. Unique to *C. rastrospinosus* the diversity for SO was higher than for AP.

mtDNA: genetic population structure

Power analyses revealed poor capabilities of the mtDNA sequences to detect subtle differentiations among populations for both D-loop and cyt *b*. High probability to detect true differentiation as low as $F_{ST} = 0.01$ was only evident for *G. gibberifrons* (Online Resource 4). Fine-scale genetic differentiations measured as pairwise F_{ST} between sampling localities (AP, EI and SO) were neither high nor significant for any species (data not shown). We therefore combined the AP and EI samples to test differentiation along the prevailing current from the AP/EI region toward SO. After pooling, differentiation between sample localities remained non-significant and ranged between −0.003 ($p = 0.48$) for *C. gunnari* and 0.04 ($p = 0.06$) for *C. rastrospinosus* (Table 2). The constructed haplotype genealogies support these findings and reflect genetic diversity rather than differentiations between localities (Fig. 3).

Microsatellites: genetic diversity and demographic history

Microsatellites were successfully genotyped for 56 (*C. rastrospinosus*) to 125 individuals (*C. aceratus*) per species (Online Resource 1). Individuals with missing data at one or more loci were excluded from the analyses. Significant genotypic linkage disequilibrium between loci was limited to the pair of Cr236 and Trne20 in *C. gunnari* ($p = 0.03$; data not shown). On the species level, for all but *T. newnesi* the hypothesis of HWE could be rejected (data not shown) and null alleles might be present at least at one locus in every pertained species (Online Resource 5). On the population level, HWE is only evident for both *T. newnesi* populations and the EI samples of *C. aceratus* (Online Resource 6). The null alleles found in this study are probably a result from the cross-species amplifications with microsatellite primers that were originally isolated from other notothenioid species. Among all species, *G. gibberifrons* had the highest (24.0 ± 14.0) and *C. gunnari* the lowest (10.7 ± 7.7) allelic richness (data not shown).

Reductions in population size were examined for species and populations. On the species level, none showed signs of a bottleneck concurrently in all three indicators examined (Online Resource 7). The probability of heterozygosity excess was significant only in *C. gunnari* and *C. rastrospinosus* (both $p < 0.01$), while the Garza-Williamson index

Table 2 Population differentiation (*F*-statistics) between Antarctic Peninsula and South Orkney Islands samples based on mtDNA and microsatellites

	Species						
	C. aceratus	*C. gunnari*	*C. rastrospinosus*	*G. gibberifrons*	*L. squamifrons*	*T. eulepidotus*	*T. newnesi*
mtDNA							
F_{ST}	−0.0056	−0.0027	0.0440	0.0027	−0.0087	−0.0053	−0.0146
Microsatellites							
F_{ST}	0.0088*	0.0226**	−0.0004	0.0002	−0.0015	−0.0035	0.0067
F_{ST} ENA	0.0088	0.0219	0.0021	0.0002	−0.0006	−0.0018	0.0027
F_{IS}	0.022*	0.034*	0.182**	0.062**	0.074**	0.161**	0.006
F_{IT}	0.03*	0.06*	0.18*	0.06*	0.07*	0.16*	0.01

ENA excluding null alleles

ENA results without significances, AMOVA significances: * $p \leq 0.05$, ** $p \leq 0.01$

was low (0.48 ± 0.21) only in *T. newnesi*. For every species, the frequency distributions of alleles were normal L shaped. On the population level, the only sample, which showed evidence for a recent bottleneck in all tests, was *T. newnesi* from the SO shelf. In *C. gunnari* from SO heterozygosity excess and mode shift were evident, but the Garza-Williamson index was relatively high (0.63 ± 0.20).

Microsatellites: genetic population structure

The power of the microsatellites to detect significant population differentiation was generally much higher than for mtDNA sequences. Simulations suggest an average probability of 97% to detect a true differentiation of $F_{ST} = 0.01$ resulting from both the chi-squared (SD = 0.03) and Fisher's exact (SD = 0.02) tests (Online Resource 4).

Population structure based on microsatellites was assessed with AMOVA (Table 2) and in a Bayesian approach (Table 3). Similar to mtDNA sequences, we found no significant differentiation between sampling localities of the AP and EI region (data not shown) and therefore combined these samples to test the genetic structure along the current system. In congruence with mtDNA data, differentiations between AP/EI and SO populations were minor in every species. Indeed, F_{ST} values were mostly one order of magnitude lower than for mtDNA except for *C. aceratus* and *C. gunnari*. These two species were also the only ones showing significant differentiation. Excluding null alleles from analyses did not alter the previous findings of low differentiation in any species, although it also changed F_{ST} values in some cases by one order of magnitude. The overall genetic variation can rather be explained by larger differences between individuals than between populations.

Drifter analyses

Between 15 February 1979 and 31 December 2009, a total of 73 drifters crossed the AP, EI, and SO shelf areas (Fig. 2). Out of 64 drifters leaving the AP and EI shelf areas, one reached the SO shelf after 46 days, which is shorter than most notothenioid larval stages. This drifter had left the AP shelf at its easternmost end on 30 January 2008 and crossed the Philip Passage perpendicular to Weddell Sea Deep Water outflow (Heywood et al. 2002). This may have been facilitated by wind-driven surface currents and indicates that dispersal of passive particles from AP/EI to SO shelf areas is possible albeit comparatively rare. Most other drifters leaving the AP/EI shelf areas took a more northerly route in the ACC's main current and missed the SO shelf. Drifters leaving the SO shelf area dispersed in a northeastern direction, and none of them reached the AP/EI region.

Microsatellites and mtDNA: isolation-with-migration model

The IM model was used to test whether gene flow is unidirectional with the prevailing current as expected by gene flow through passive larval dispersal or bidirectional through gene flow by adult migration. In congruence with our *F*-statistics, IMa2 did only resolve gene flow in *C. aceratus* and *C. gunnari*, for which significant population differentiation could be found. The remaining species either showed no migration or their time since divergence was about zero (Table 4). Hence, IMa2 was not able to calculate migration rates when gene flow is too high and there is no clear separation between populations. In the following, we therefore present and discuss the isolation-with-migration results only for *C. aceratus* and *C. gunnari*. The migration parameters m_1 (from SO to AP/EI) and m_2 (from AP/EI to SO) derived from the models indicate asymmetric gene flow with the current in both species (Table 4; Online Resource 8). Calculated population migration rates (effective rates at which genes come into populations per generation; M_1, M_2) show a distinct pattern of gene flow with the current

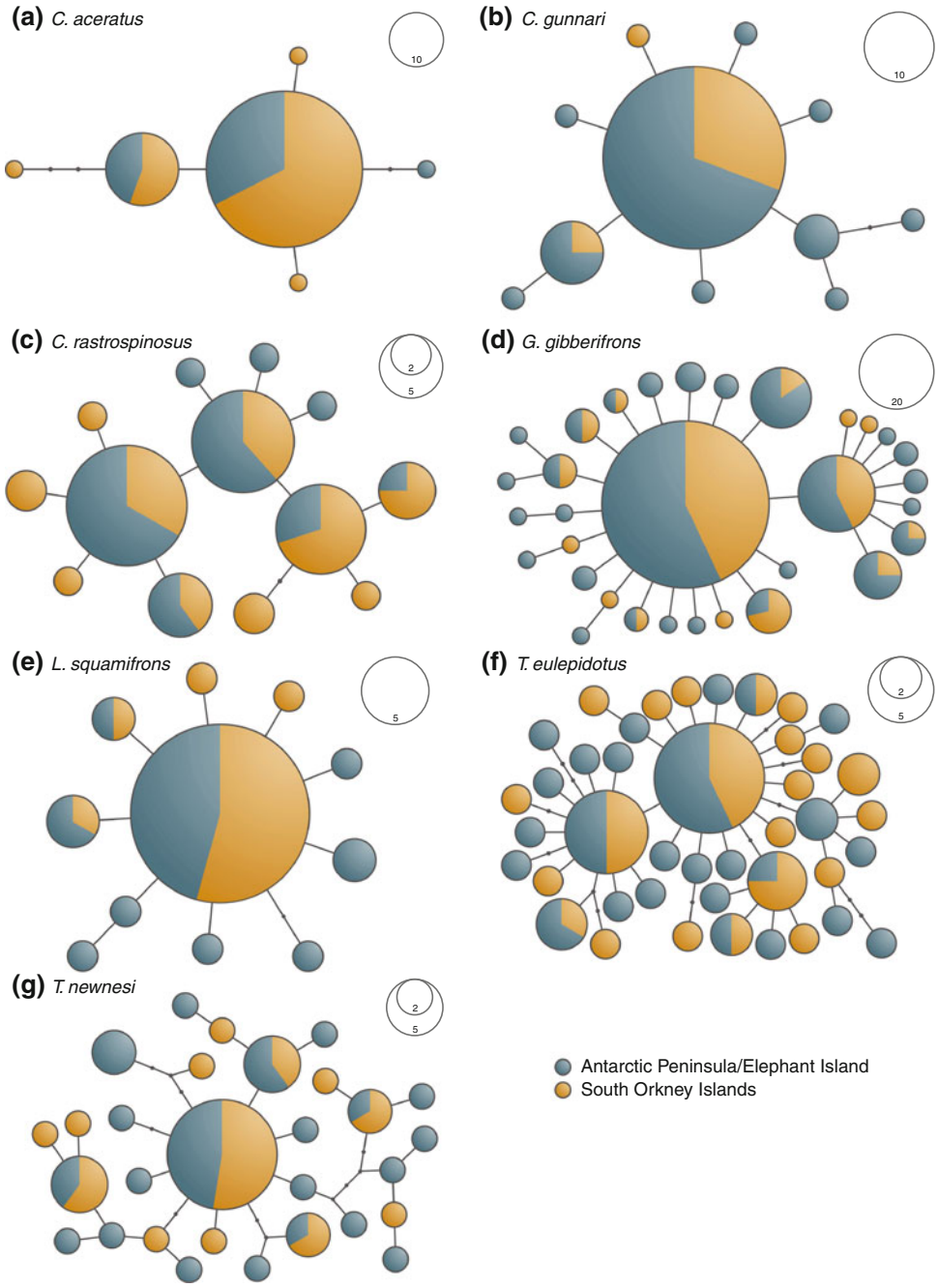

Fig. 3 Unrooted haplotype genealogies based on mitochondrial D-loop (**a**–**d**) and cyt *b* sequences (**e**–**g**). Radii reflect number of individuals

from AP/EI to SO, but are negligible from SO to AP/EI. With regard to private alleles in microsatellites, which may indicate a source–sink relationship by holding more unshared alleles in populations that act as sinks (and are usually found downstream), there is no uniform coherence between the direction of gene flow according to IMa2 estimates and the number of private alleles per population.

Discussion

Genetic structure and diversity

The results obtained in the present study show low or non-existing genetic population differentiation for seven of the most abundant notothenioid species in the southern Scotia Arc. These results seem to be independent of the adult life

Table 3 Number of clusters with highest mean posterior probability inferred from Bayesian analyses as indicated by ΔK (maximum ΔK in parenthesis)

	Species						
	C. aceratus	*C. gunnari*	*C. rastrospinosus*	*G. gibberifrons*	*L. squamifrons*	*T. eulepidotus*	*T. newnesi*
INA	1 (30.6)	1 (48.8)	2 (147.3)	1 (130.9)	1 (4.5)	2 (31.1)	1 (20.0)
INA locprior	1 (8.1)	1 (63.2)	1 (93.6)	1 (5.7)	1 (7.2)	1 (23.1)	1 (44.1)
ENA	1 (12.9)	1 (7.3)	2 (52.4)	1 (157.8)	1 (9.0)	1 (11.1)	No NA
ENA locprior	1 (88.7)	1 (69.3)	1 (63.0)	1 (9.8)	2 (1.0)	1 (12.9)	No NA

INA including null alleles, *ENA* excluding null alleles (according to MicroChecker 2.2.3), *locprior* a priori information of sampling sites incorporated in analysis

Table 4 Isolation-with-migration results reflecting parameter bins with highest posterior probabilities (high points)

Species	Parameter							
	t0	Θ1	Θ2	ΘA	m1	m2	M1	M2
C. aceratus	0.129	7.25	14.74	141.20	0.05	4.55	0.18	33.56
C. gunnari	0.443	4.75	2.75	52.25	0.05	2.65	0.12	3.64
C. rastrospinosus	0.001	74.75	23.75	47.25	0.05	0.05	1.87	0.59
G. gibberifrons I	0.001	71.25	17.25	21.25	0.05	0.05	1.78	0.43
G. gibberifrons II	0.001	125.80	21.25	46.75	0.05	0.05	3.15	0.53
L. squamifrons	0.001	35.00	15.00	55.00	0.05	0.05	0.875	0.375
T. eulepidotus	0.193	25.00	375.00	35.00	0.05	0.05	0.625	9.375
T. newnesi	0.002	37.50	16.50	360.50	3.85	0.05	72.188	0.413

t0 = time since divergence, Θ1 = effective AP/EI populations size, Θ2 = effective SO populations size, ΘA = effective ancestral populations size, m1 = migration rate from SO to AP/EI, m2 = migration rate from AP/EI to SO, M1 and M2 = accordant population migration rates

history strategies but are accordant to expectations for marine species with long pelagic larval stages. Both types of genetic markers used in this study show either no or only weak genetic structure among populations for all studied species. None of the obtained haplotype genealogies based on mtDNA shows a clear separation between localities (Fig. 2) and *F*-statistics for both markers revealed, if at all, only minor differentiations. The only significant differentiations were found within the channichthyids, *C. aceratus* and *C. gunnari*, while *C. rastrospinosus* and the nototheniid populations of *G. gibberifrons*, *L. squamifrons*, *T. eulepidotus*, and *T. newnesi* generally lack a clear genetic structure. However, the channichthyid differentiations are not congruent among marker types and can therefore be used to discriminate between short- and long-term population dynamics. Microsatellites evolve faster than mtDNA and their higher diversities allow to infer present connectivity patterns better than mtDNA, which carries a longer-persisting signature of past events (Selkoe and Toonen 2006). Historical or long existing barriers to gene flow are hence more likely to be detected with mtDNA sequences. In our data, significant differentiations with microsatellite markers between samples from the AP/EI region and SO were only detected in the benthic *C. aceratus* and the benthopelagic *C. gunnari*. However, the differentiation observed in both species is only minor. Our cluster analyses with the software STRUCTURE suggest in both cases the existence of only one population in the study area. As indicated by the low genetic differentiations measured by F_{ST}, STRUCTURE may not have been able to resolve the populations as separate entities. The small differentiations detected with mtDNA indicate homogenizing gene flow between AP/EI and SO. The highest differentiation of mtDNA sequences was found in the benthopelagic *C. rastrospinosus* ($F_{ST} = 0.04$), but even for this species, the differentiation was not significant. Although the differentiation measured by microsatellite data was close to zero in *C. rastrospinosus*, which indicates that the true differentiation might not be as high as measured with mtDNA, their power to detect subtle population differences was rather low in this case. Differences in the cluster analyses between runs including and excluding information about sampling localities, which result in one and two clusters, respectively, suggest that a possible differentiation in *C. rastrospinosus* is more likely based on unrecognized factors (as e.g., sampling of cohorts) than geographically separated populations. In the four notothenid

species *G. gibberifrons, L. squamifrons, T. eulepidotus* and *T. newnesi*, the genetic differentiations between localities are generally low and not significant giving little evidence for the existence of barriers to gene flow between shelf areas in the southern Scotia Arc.

Our results add new information on the connectivity of notothenioid populations in the area. Previous studies on notothenioid population structures along the Scotia Arc were based on parasite infestation rates (Kock and Möller 1977; Siegel 1980a), morphometric characters (Kock 1981), and more recently on a variety of genetic markers (e.g. Papetti et al. 2009). Studies based on parasite infestation rates revealed differences between populations north and south of the ACC in *C. gunnari* and *C. aceratus*, but not among populations of *C. aceratus* and *C. rastrospinosus* along the southern Scotia Arc (Kock and Möller 1977; Siegel 1980a, b). For *C. gunnari*, four different populations had been identified based on morphometric characters from South Georgia, SO, SSh, and EI (Kock 1981). Significant differentiation was also confirmed with genetic marker sets for *C. gunnari* populations north and south of the ACC (Kuhn and Gaffney 2006), but the island shelves along the southern Scotia Arc had not yet been compared. A recent publication on the genetic population structure of *C. aceratus* from the southern Scotia Arc based on microsatellites is in agreement with our results and shows that the populations on both sides of the Philip Passage are weakly, but significantly differentiated, while migration is still evident (Papetti et al. 2009). In our study, significant genetic differentiation in *C. aceratus* was detected with microsatellites, but not with mtDNA sequences. Hence, in the long run, the migration rates in this sedentary species seem to be high enough (e.g., >1 individual per generation Mills and Allendorf 1996) to counteract genetic drift and population differentiation. Microsatellite fragment lengths are susceptible to changes in frequency with every generation and *F*-statistics rather show a captured moment of population structure than history. Overall, the generally low genetic differentiation suggests high connectivity between populations in the study area.

With regard to the mutation rates of microsatellites and mtDNA, it seems to be counterintuitive that genetic differentiations between populations measured with fast evolving microsatellites are smaller than for slower evolving mtDNA as observed in *C. rastrospinosus* and to a lesser extent in *G. gibberifrons* and *T. newnesi*. A similar pattern was already observed in populations of *D. eleginoides* from Heard and McDonald Island, Macquarie Island, and South Georgia (Appleyard et al. 2002). Different genetic patterns between maternally inherited markers such as mtDNA and bi-parentally inherited markers such as nuclear microsatellites can arise from sexual differences in spawning behavior or simply by genetic drift and population bottlenecks. Maternally inherited mtDNA is more affected by the latter two than nuclear DNA, since its effective population size is only one quarter that of nuclear DNA, which may result in higher divergences for mtDNA. Of the three species showing this discrepancy between markers in our study, spawning migrations are only known for *C. rastrospinosus*, which migrates to shelf waters of 200–300 m depth to spawn (Kock 1989). However, it is currently unknown whether *C. rastrospinosus* prefers specific spawning grounds and whether sexual differences in migration behavior exist (Kock 2005a), leaving this explanation to speculation. By contrast, for all three species, at least one bottleneck indicator suggests that populations might have undergone a reduction in population size. We therefore cannot exclude bottlenecks and genetic drift as possible reasons for this pattern. However, these unusual differences between markers do not affect our general finding of low or absent population structure in the southern Scotia Arc.

According to genetic studies from the last decade, the levels of population differentiation in notothenioids vary widely and do not show a universal pattern. These studies primarily focused on single species targeted by the fisheries industry in the Southern Ocean like *C. gunnari*, *D. eleginoides*, or *D. mawsoni* (Smith and McVeagh 2000; Appleyard et al. 2002; Parker et al. 2002; Shaw et al. 2004; Smith and Gaffney 2005; Rogers et al. 2006; Kuhn and Gaffney 2006, 2008), and their results depend on the types of genetic markers used (allozymes, RAPDs, microsatellites, mt and nuclear DNA sequences). Although most species show genetic differences between single populations, a lack of differentiation over large parts of even circum-Antarctic distribution ranges is evident. In this regard, the adult life history strategy and habit seem to play only a minor role for the genetic structuring of populations, since this pattern can be found not only in active pelagic swimmers as the Antarctic silverfish *Pleuragramma antarcticum* (Zane et al. 2006), but also in strictly benthic species as *G. gibberifrons* (Matschiner et al. 2009). It seems plausible that gene flow between populations of notothenioids is primarily based on larval dispersal. Hence, oceanography is a key factor influencing the structure of notothenioid populations.

Migration and gene flow

The genetic population structures found in this study revealed ongoing gene flow in the southern Scotia Arc for all study species, regardless of their adult habit or larval stage duration. For the channichthyids *C. aceratus* and *C. gunnari*, unidirectional gene flow from AP/EI to SO coincides with the current pattern of the ACC in the study area. Advection of eggs and pelagic larvae with the current is therefore a likely key feature connecting populations of notothenioid species that are bound to shelf and slope

habitats during their adult stage. The pelagic phase of larvae takes about 400–500 days in *C. aceratus* (La Mesa and Ashford 2008b), but exact data for *C. gunnari* are still lacking. At South Shetlands, *C. gunnari* spawns its eggs freely into the water in June–July and hatching occurs in January–March, leaving a time frame of about 8 months in which eggs may be dispersed. Young juveniles caught with a bottom trawl at South Georgia were estimated to be 3.5–6.5 months old (North 2005). If growth rates are comparable between regions, the pelagic phase of *C. gunnari* may hence be completed within 11.5 months (or about 350 days). Since both species have an absolute fecundity in the same order of magnitude, the amount of larvae reaching the other shelf should be comparable or slightly less in *C. gunnari*. But as our results show, the migration rate of *C. aceratus* is about twice as high as in *C. gunnari*. This may indicate that the eggs of *C. gunnari* stay near the ground and are less advected by the current than the larvae, reducing the time of possible dispersal and raising genetic heterogeneity between populations. To this point, the role of putative differences between egg and larval dispersal on population structuring remains an open question and needs further investigations.

Overall, we conclude that the general pattern of weak or absent genetic population structure found for notothenioids with differing adult life history strategies is primarily based on the characteristic they all have in common, the pelagic larval phase. With regard to the adaptive radiation of notothenioids, it remains unclear how species evolve rapidly while differentiation is counteracted by high gene flow through larval dispersal. It seems likely that notothenioid speciation events are restricted to periods when larval dispersal is hindered as, for example, during extended ice-coverages in the course of glacial maxima. To further examine the role of larval dispersal on population structure and adaptive radiation in notothenioids, it is necessary to conduct further comparative population genetic studies over wider geographic scales including hydrographic features like the ACC.

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