Distribution and zoogeographic affinities of the nudibranch fauna (Mollusca, Opisthobranchia, Nudibranchia) of the Faroe Islands

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Abstract

Distribution of nudibranchs (Mollusca, Opisthobranchia, Nudibranchia) from the BIOFAR1 and BIOFAR2 projects are presented on a local scale, i.e. in Faroese waters, and on a global scale. The global zoogeographic affinities are discussed in relation to different hypotheses for colonisation and/or vicariance. BIOFAR1 collected about 40 species, some of which could only be identified to genus, with a total of 354 specimens of nudibranchs from 54 stations. BIOFAR2 collected about 25 species with a total of 249 specimens from 89 samples. The total number of species of nudibranchs in Faroese waters is now 51. Few nudibranch species show a distinct distribution pattern at the local scale, either with respect to depth or temperature. At the North Atlantic regional scale, almost all of the Faroese nudibranchs also occur along the coast of Norway and/or the British Isles. The highest similarity is with the nudibranch fauna of northern Norway. Only one truly arctic species was found in the BIOFAR1 material. Some species are northern hemisphere cosmopolitans and are both eurythermal and eurybathic. Some species are restricted to depths greater than 70 m, and some are restricted to shallow waters.

Introduction

The BIOFAR projects (1987-90 and 1995-98) have provided a large material of Nudibranchia (Mollusca; Opisthobranchia) (Sneli *et al*., 2005), which has enabled a more detailed analysis of the geographic distribution of these animals. Although no new (undescribed) species have been identified, known ranges of distribution have been extended for several species. Also, species that have previously been considered very rare have been found in larger numbers, and it is now possible to identify some of their habitat requirements.

Several theories have been proposed to explain current patterns of distribution for marine organisms. Traditional island biogeography theory states that the number of species decreases with distance from the continent and that the number of species increases with increasing area of the island (MacArthur and Wilson, 1967). In the case of marine benthic species this means the area of suitable depth. Colonisation of oceanic islands can take place through dispersal of planktonic larvae or rafting of adult animals. As the duration of planktonic stages may not be long enough for trans-

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port from the continent to oceanic islands, a step-wise colonisation through "island-hopping" has been proposed (Leal and Bouchet, 1991). Finally, the number of endemic species has been used as an indicator of the duration of geographic isolation of the islands, but again, area will affect the likelihood for speciation (Sadler, 1999).

Nudibranchs are notoriously difficult to identify from preserved material, and in the case of the BIOFAR material, collecting and processing of samples have been very rough on these soft-bodied animals. Also, taxonomy is unsettled for some genera. In *Doto* new species have recently been described almost exclusively based on molecular differences (Morrow *et al*., 1992). Hence the species here identified as *Doto coronata?* may consist of more than one species. On the other hand, several poorly described species have been synonymized with more common and well-described species (Kuzirian, 1979). Possibly this has been premature.

In the present paper the species of Nudibranchia (Mollusca, Opisthobranchia) will be listed with their distribution in the Faroe Islands as well as global distribution. Zoogeographic affinities will be discussed in relation to depth, temperature and life history.

Methods

Identification of preserved specimens was based on external examination and, in a few cases, on radular and other anatomical characters. As many specimens, especially aeolids, were very small (1-2 mm) and/or badly mangled, and in most cases only one specimen was available from one station, some animals could only be identified to genus. These records were excluded from calculations of similarity.

For zoogeographic analysis the BIOFAR species were compared with the species found in other northern hemisphere regions. The nudibranch fauna of the British Isles (Thompson and Brown, 1984; Picton and Morrow, 1994) is probably the best documented and hence this has been used as a baseline. Distribution data were taken from the literature. Similarity of the Faroese nudibranch fauna with that of other regions was calculated by Jaccard's coefficient (Valentine, 1966) and the Dice coefficient (Leal and Bouchet, 1991). Also, the Inclusion Index of Golikov (1989) was calculated. The regions used for comparison were: (1) the British Isles, (2) southern Norway (sectors 1-15 of Brattegard and Holthe, 2001), (3) northern Norway (sectors 16-26 of Brattegard and Holthe, 2001; Evertsen and Bakken, 2002), (4) Spitzbergen (Gulliksen *et al*., 1999), (5) Iceland (Lemche, 1938; Platts, 1985), (6) eastern Greenland and Jan Mayen (Lemche, 1941a; Sneli and Steinnes, 1975; Gulliksen *et al*., 1999), (7) western Greenland (Lemche, 1941b; Platts, 1985), (8) eastern Canada to Cape Cod (USA) (Bleakney, 1996), (9) Alaska and western Canada to Oregon (USA) (Lee and Foster, 1985; Behrens, 1991), (10) northern Japan (Baba, 1957; Hirano, 1997; 1999; Hirano and Hirano, 1990; Hirano and Kuzirian, 1991), (11) Arctic waters north of Siberia and Russia (Sea of Okhotsk to Barents and White Seas) (Odhner, 1907; Roginskaya, 1962;

1971; 1997). The selection of sectors 15 and 16 (Brattegard and Holthe, 2001) for separating southern and northern Norway is not entirely arbitrary as 17 of 43 southern species have their northern limit in sectors 13-16; only 8 species have their northern limit in sectors 17-19 and 9 species in sectors 10-12. Of the 9 northern species, only one occurs south of sector 16. For the Faroe Islands, previous records (Lemche, 1929; Platts, 1985) were included as well as the species collected by the BIOFAR projects. Synonymies and nomenclatural changes were taken from the most recent literature available, including entries on the Sea Slug Forum (http://www.seaslugforum.net/).

***Table 1**. Species diversity of Nudibranchia in the BIOFAR1 (1987-90) and BIOFAR2 (1994-97) projects.*

	BIOFAR1	BIOFAR2
Number of stations	790	872
% stations with nudibranchs	6.6	10
Max. no. species/station	12[a]	6[b]
Max. no. specimens/station	114[a]	25[b]
Max. no. specimens/species/ station	48[a]	17[b]
Total no. species	ca. 40	ca. 25
Total no. genera	23	17
Total no. families	16	12
Total no. specimens	354	249

[a]Station 56. [b]Station 1176.

Results

Local distribution and abundance

Spatial variations. The BIOFAR1 project took a total of 790 samples between 1987 and 1990 (Nørrevang *et al*., 1994). Of these, 54 (6.6 %) contained a total of 354 specimens of Nudibranchia, belonging to about 40 species (some could only be identified to genus level), 23 genera in 16 families (Table 1). Several types of gear were used, but two in particular were suitable for collecting nudibranchs: The modified Rothlisberg and Pearcy epibenthic sampler was used for 76 samples (Nørrevang *et al*., 1994). Nineteen of these (25 %) contained nudibranchs. The detritus sledge was used for 165 samples of which 25 (15 %) contained nudibranchs, whereas the triangular dredge, which was used for 214 samples, only collected nudibranchs in seven samples (3.3 %). Most samples (29) contained only one species, and the majority of these (21) contained only one specimen. Station 56 contained 12 different nudibranch species and a total of 114 specimens, i.e., almost one third of the total number of species and specimens. For 9 species only one specimen was collected, and 12 species were only collected from one station. The most common species were *Doto coronata?* (N=78), *Dendronotus frondosus* (N=35) and *Flabellina (=Coryphella) verrucosa* (N=31). The most "widespread" species were *Cadlina laevis*, which was found at 12 stations, and *Flabellina verrucosa*, which was found at 11 stations. *Aldisa zetlandica* and *Dendronotus frondosus* were found at 8 stations each, and *Flabellina (=Coryphella) nobilis* and *Triopella incisa* were found at five stations each. In the BIOFAR1 material 23 specimens of *Aldisa zetlandica* were identified from 8 stations, 6 of which were deeper than 400 m, and only one was east of the Faroe Islands. Most were located along the deep channel separating the Faroe Islands from the Faroe

Table 2. *Yearly variation in nudibranch diversity in the catches of BIOFAR1 (1987-90) and BIOFAR2 (1995-98) projects.*

year	no. species	no. specimens
1987	27	215
1988	20	107
1989	8	30
1990	2	2
1994	5	16
1995	18	70
1996	20	110
1997	12	53

Bank, close to the areas identified as "ostur", i.e. bottom fauna dominated by massive, cheese-like sponges (Klitgaard and Tendal, 2001). *Aldisa zetlandica* is a sponge feeder, but its food has not been identified (Millen and Gosliner, 1985).

BIOFAR2 sampled 872 stations from depths between 0 and 100 m (Sørensen *et al*., 2001). Collecting gears differed from BIOFAR1, and a large number of samples were taken by Scuba diving (543) or by hand collecting (108) in the intertidal zone. A total of 249 nudibranch specimens belonging to about 25 species (again some could only be identified to genus), 17 genera in 12 families, were found in 89 samples (~10 % of samples) (Table 1). Station 1176 contained six species (25 specimens), station 1395 had five species (six specimens) and stations 1431, 1497 and 1620 each contained four species (six, five and seven specimens respectively). Seven stations contained three species, 11 stations contained two species, and the remaining 66 stations contained only one species; 43 of these had only one specimen. The most common species were *Dendronotus frondosus*, which was found in 20 samples (N=32), *Doto coronata?* found in 12 samples (N=42), *Archidoris pseudoargus* found in 11 samples (N=18), and *Onchidoris bilamellata*, which was found in 10 samples (N=14). Almost all of the species occurred in more than one sample and only two species were represented by a single specimen. This probably reflects the more selective and gentle collecting methods employed.

Temporal variations. Few samples were taken during the winter, but the percentage containing nudibranchs did not differ from that of summer samples. The majority of nudibranchs were collected in 1987 (Table 2). In succeeding years the number of species and specimens decreased, and in 1990 only two species with two specimens were collected. Six species were collected in three of the four years, 12 species in two years and 18 in only year (Table 3). During BIOFAR2, the number of species and specimens increased over the years 1994-96 but decreased in 1997 (Table 2). Eleven species were found in three years, five species in two years and seven in one year. The species identified as *Doto coronata*? was collected in all four years, but this species may contain more than one cryptic species. Of the 35+ species found in BIOFAR1, 17 did not occur in the BIOFAR2 material; conversely, six of the 24 species found in BIOFAR2 did not occur in the BIOFAR1 material. Abundance data for all nudibranchs collected in the BIOFAR projects are shown in Table 3. About 10 further species that have been recorded from the

Table 3. *Local distribution of nudibranchs from BIOFAR1/ BIOFAR2 projects. For each parameter, the first number designates the frequency of occurrence in BIOFAR1 samples and the second number the frequency of occurrence in BIOFAR2 samples.*

Species	number of stations	number of specimens	no. months	no. years
Acanthodoris pilosa (Müller, 1789)	2/2	3/2	1/1	2/1
Aeolidia papillosa? (Linnaeus, 1761)	0/1	0/1	0/1	0/1
Aldisa zetlandica (Alder and Hancock, 1854)	8/0	23/0	3/0	3/0
Ancula gibbosa (Risso, 1818)	0/2	0/2	0/1	0/1
Archidoris pseudoargus (Rapp, 1827)	2/11	2/18	1/3	2/3
Cadlina laevis (Linnaeus, 1767)	12/7	18/9	2/3	2/2
Cuthona sp.	2/2	2/3	1/1	1/2
Dendronotus frondosus (Ascanius, 1774)	8/20	35/32	2/3	3/3
Doridoxa ingolfiana Bergh, 1899	1/0	1/0	1/0	1/0
Doto cf. *cuspidata* Alder and Hancock, 1862	2/0	6/0	2/0	1/0
Doto coronata? (Gmelin, 1791)	4/12	78/42	2/2	2/4
Doto crassicornis M. Sars, 1870	2/0	3/0	1/0	1/0
Doto sp.	5/9	29/28	2/3	3/3
Eubranchus exiguus (Alder and Hancock, 1848)	2/0	2/0	1/0	2/0
Eubranchus pallidus (Alder and Hancock, 1842)	1/0	12/0	1/0	1/0
Eubranchus tricolor Forbes, 1838	3/2	3/2	1/2	1/1
Eubranchus sp.	1/7	7/13	1/3	1/3
Facelina sp.	1/0	1/0	1/0	1/0
Flabellina gracilis (Alder and Hancock, 1844)	1/1	1/1	1/1	1/1
Flabellina nobilis (Verrill, 1880)	5/8	9/11	2/3	2/3
Flabellina pellucida (Alder and Hancock, 1843)	2/0	6/0	1/0	1/0
Flabellina verrucosa (M. Sars, 1829)	11/5	31/12	2/5	2/2
Flabellina spp.	4/6	18/9	2/3	2/3
Goniodoris nodosa (Montagu, 1808)	0/3	0/10	0/3	0/3
Hero formosa (Lovén, 1841)	2/0	5/0	1/0	1/0
Jorunna tomentosa (Cuvier, 1804)	4/0	4/0	2/0	3/0
Limacia clavigera (Müller, 1776)	3/4	15/4	2/3	2/3
Lomanotus genei Verany, 1846	1/0	1/0	1/0	1/0
Lophodoris danielsseni (Friele and Hansen, 1876)	2/0	7/0	1/0	1/0
Okenia aspersa (Alder and Hancock, 1845)	2/0	3/0	1/0	2/0
Onchidoris bilamellata (Linnaeus, 1767)	0/10	0/14	0/4	0/3
Onchidoris muricata (Müller, 1776)	1/6	1/11	1/3	1/3
Onchidoris oblonga (Alder and Hancock, 1845)	3/0	4/0	3/0	3/0
Onchidoris sp.	1/0	1/0	1/0	1/0
Palio dubia (M. Sars, 1829)	0/4	0/6	0/2	0/2
Polycera faeroensis Lemche, 1929	1/0	1/0	1/0	1/0
Tenellia adspersa (Nordmann, 1845)	1/3	2/7	1/1	1/3
Tergipes tergipes (Forsskål, 1775)	0/1	0/3	0/1	0/1
Triopella incisa (G.O. Sars, 1872 ex M. Sars, MS)	5/0	7/0	2/0	2/0
Tritonia hombergi Cuvier, 1803	1/4	1/6	1/3	1/2
Tritonia plebeia Johnston, 1828	4/1	7/3	3/1	3/1
Tritonia sp. A	2/0	4/0	2/0	2/0

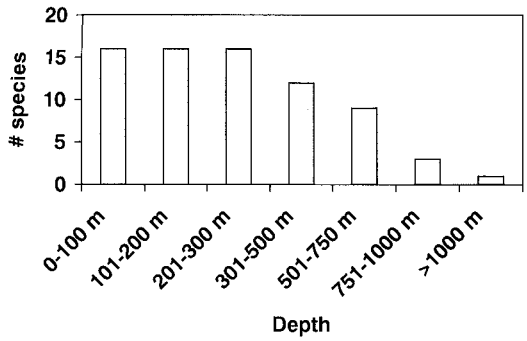

Figure 1. *Depth distribution of nudibranch species from BIOFAR1.*

Faroe Islands previously, were not found in either BIOFAR1 or BIOFAR2.

Depth distributions. BIOFAR1 stations ranged in depth from 20 to 2420 m, but only 13 stations were taken at depths over 1200 m (Nørrevang *et al.*, 1994). Nudibranchs were found in samples from 73 m to 1096 m. Species abundance at different depths is shown in Figure 1. Eight species were found exclusively at depths lower than 200 m, and 17 species occurred at depths greater than 300 m. *Triopella incisa* occurs almost exclusively at depths over 200 m, and most specimens of *Aldisa zetlandica* were found at depths greater than 400 m. Depth ranges for all species found at more than one station are shown in Table 4. The greatest depth for *Okenia aspersa* was given as 60 m (Thompson and Brown, 1984). The BIOFAR specimens were collected at 185 and 240 m. Six species have depth ranges of more than 500 m, and four species have depth ranges of 300 to 500 m. BIOFAR2 stations extended from the intertidal to 119 m (plus a few between 120 and 595 m) (Sørensen *et al.*, 2001) and nudibranchs were found from the intertidal to 100 m.

Distribution in relation to temperature. Temperature was only recorded for BIOFAR1 stations (Nørrevang *et al.,* 1994). Temperature ranges for species found at more than one station are listed in Table 4. The species with the widest depth ranges are also the ones that have the largest temperature ranges. Most species are restricted to the warm Atlantic water with temperatures above 7 °C (Westerberg, 1990). Only the eurythermal species and the arctic *Doridoxa ingolfiana* (603 m and 0 °C) occurred in the cold Norwegian Sea deep water (below 0 °C) or in mixed Norwegian Sea and North Icelandic/Arctic intermediate water (0-2 °C) (Westerberg, 1990).

Global distributions

Prior to BIOFAR 35 species of Nudibranchia had been recorded from the Faroe Islands (Lemche, 1929; Platts, 1985). Now the total number of species has increased to 51 (Table 5). Six species have an almost ubiquitous (circumboreal-arctic) northern hemisphere distribution (Thompson and Brown, 1984; Behrens, 1991). They occur in arctic as well as temperate waters, and *Acanthodoris pilosa* even reaches into the Mediterranean. Six species are amphi-Atlantic and also occur in the Northeast Pacific Ocean (Lee and Foster, 1985; Platts, 1985; Millen, 1989; Bleakney, 1996). These also extend into arctic waters (Roginskaya, 1962; 1969), but none of them have been found in the Mediterranean

Table 4. *Depth and temperature ranges for nudibranchs from the BIOFAR programme. Species found at only one station have been omitted.*

Species	BIOFAR1 depth range (m)	BIOFAR1 temp. range (°C)	BIOFAR2 depth range (m)
Acanthodoris pilosa	514-923	3-8.6	5-20
Aldisa zetlandica	218-725	1.5-7.7	-
Ancula gibbosa	-	-	10-20
Archidoris pseudoargus	80-604	0-7.9	5-20
Cadlina laevis	73-997	3.1-8.2	5-15
Cuthona sp.	150-218	7.6-7.9	15
Dendronotus frondosus	77-1096	-0.84-8.1	0-70
Doto cf. *cuspidata*	80-96	7.9-8.7	-
Doto coronata?	77-276	6.5-8.5	0-70
Doto crassicornis	150-283	6.8-7.9	-
Doto sp.	77-430	6-8	0-94
Eubranchus exiguus	80-322	7.9	-
Eubranchus tricolor	156-225	7.5-8.6	37-50
Eubranchus sp.	-	-	0-61
Flabellina nobilis	205-507	1-7.9	5-71
Flabellina pellucida	218-283	6.8-7.6	-
Flabellina verrucosa	73-350	6.8-8.6	20-100
Flabellina spp.	150-683	-0.5-7.9	5-68
Goniodoris nodosa	-	-	2-15
Hero formosa	218-276	6.5-7.6	-
Jorunna tomentosa	121-604	0-7.9	-
Limacia clavigera	77-107	7.9	5-94
Lophodoris danielsseni	77-225	7.5-7.9	-
Okenia aspersa	185-240	7.4-8.6	-
Onchidoris bilamellata	-	-	2-20
Onchidoris muricata	-	-	5-35
Onchidoris oblonga	77-150	7.9-8.1	-
Palio dubia	-	-	5-48
Tenellia adspersa	-	-	4-58
Triopella incisa	170-684	4.6-8	-
Tritonia hombergi	-	-	5-15
Tritonia plebeia	77-140	7.9-8.7	-
Tritonia sp. A	77-107	7.9	-

(Thompson and Brown, 1984). Another five species occur in the North as well as the South Atlantic Ocean (Gosliner, 1987) and also in the Mediterranean (Thompson and Brown, 1984). These species have not been recorded from arctic waters. Twelve species are amphi-Atlantic, but only four of these extend into arctic waters (White Sea) (Odhner, 1907; Roginskaya, 1962) and eight into the Mediterranean (Thompson and Brown, 1984).

The remaining species are restricted to the Northeast Atlantic Ocean, though *Lomanotus genei, Tritonia hombergi, T. ple-*

Table 5. *Global distributions of nudibranchs recorded from the Faroe Islands. + present; (A) extending into Arctic waters; (M) extending into Mediterranean; (S) extending into southern Atlantic; (B) extending into the Baltic Sea; (E) eastern part of North Pacific only.*

Species	NE Atlantic	Amphi-Atlantic	Arctic	Amphiboreal
Acanthodoris pilosa				+ (A, B, M)
Adalaria proxima				+(A, E)
Aeolidia papillosa				+ (A)
Aeolidiella glauca	+			
Aldisa zetlandica	+			
Ancula gibbosa				+(A)
Archidoris pseudoargus	+ (B, M)			
Cadlina laevis		+ (A, M)		
Cuthona abyssicola	(+)		+	
Cuthona amoena	+			
Cuthona foliata	+ (M)			
Cuthona gymnota		+ (M)		
Cuthona nana				+ (A, E)
Cuthona viridis				+ (A, E)
Dendronotus frondosus				+ (A)
Dendronotus robustus				+ (A, E)
Doridoxa ingolfiana	(+)		+	
Doto coronata		+ (S, M)		
Doto cuspidata	+			
Doto crassicornis	+			
Doto dunnei	+			
Doto fragilis	+ (M)			
Eubranchus cingulatus	+ (M?)			
Eubranchus exiguus		+ (A, B, M)		
Eubranchus pallidus		+ (M)		
Eubranchus tricolor		+ (A)		
Facelina bostoniensis		+ (M)		
Flabellina borealis	+			
Flabellina gracilis		+		
Flabellina nobilis		+		
Flabellina pellucida		+		
Flabellina verrucosa				+ (A, E)
Goniodoris nodosa	+			
Hero formosa	+			
Jorunna tomentosa	+ (M, S)			
Limacia clavigera	+ (A, M, S)			
Lomanotus genei	+ (M)			
Lophodoris danielsseni	+			
Okenia aspersa	+			
Onchidoris bilamellata				+ (A)
Onchidoris muricata				+ (A, E, B)
Onchidoris oblonga	+			
Palio dubia		+ (A, M)		
Polycera faeroensis	+			
Polycera quadrilineata	+ (M, S)			
Tenellia adspersa				+ (M)
Tergipes tergipes		+ (M, S)		
Triopella incisa	+			
Tritonia hombergi	+ (M)			
Tritonia plebeia	+ (M)			
Tritonia sp. A	+			
Total	**25**	**12**	**2**	**12**

beia, Doto fragilis, Cuthona amoena, and *C. foliata* also extend into the Mediterranean (Thompson and Brown, 1984). *Aldisa zetlandica* appears to be a deep-water species (218-725 m), but has not been recorded from arctic waters or from the deepest parts of the Norwegian Sea basin. This may be because few samples have been taken in deep water in arctic seas. Prior to the BIOFAR1 project, this species was considered rare. It has been recorded from the coast of Norway (Høisæter *et al.*, 2001), and single records exist from the Shetland Islands, northern and eastern Iceland, the North Sea and western Ireland (Thompson and Brown, 1984). There is one dubious record from Alaska (cited in Lee and Foster, 1985), which is most likely a misidentification (Millen and Gosliner, 1985). The BIOFAR material indicates that it requires relatively high current speeds and a substrate of massive sponges. *Goniodoris nodosa, Polycera faeroensis, Hero formosa, Lomanotus genei, Okenia aspersa, Onchidoris oblonga, Tritonia hombergi, T. plebeia, Doto cuspidata, D. dunnei, D. fragilis, Eubranchus cingulatus, Cuthona amoena, C. foliata,* and *Aeolidiella glauca* are distributed around the British Isles (Thompson and Brown, 1984; Platts, 1985) and, with the exception of *L. genei* and *C. amoena*, also in southern Norway (Høisæter *et al.*, 2001). Five species, *Lophodoris danielsseni, Triopella incisa, Cuthona abyssicola, Doto crassicornis* and *Flabellina borealis,* are shared between the Faroe Islands and central and northern Norway (Lemche, 1929; Platts, 1985; Høisæter, 1986). These species have not been recorded from the British Isles. The former three species occur in the Faroe Islands in relatively deep water. Thus they are probably cold-water species, which is supported by an unpublished observation that *Triopella incisa* occurs in deeper water towards the southern coast of Norway (Evertsen, *pers. comm.*). The occurrence of *F. borealis* in the Faroe Islands has been doubted; it may be based on a misidentification (Kuzirian, 1979). It was not identified in the BIOFAR material, but may be present among the specimens identified only to genus level.

Only *Cuthona abyssicola* and *Doridoxa ingolfiana* can be said to be arctic species. Both are poorly known and may be quite rare. The latter species occurs in western Greenland and in Iceland (Lemche, 1941b) and the BIOFAR1 specimen is a new record for the Faroe Islands (Sneli *et al.*, 2005). The only other species of *Doridoxa* occurs in deep water off the coast of South Africa (Schrödl *et al.*, 2001). *Cuthona abyssicola* occurs in eastern Greenland, Iceland and the Faroe Islands (Platts, 1985); another deep-water species, *C. norvegica,* occurs in northern Norway (Platts, 1985; Høisæter *et al.*, 2001). These two species are ancestral ("primitive") representatives of the genus and were originally described in a separate genus, *Cuthonella,* but this was included in *Cuthona* by Millen (1986).

Discussion

The Faroe Islands originated through vulcanic eruptions about 65 million years ago. If they had been isolated from other landmasses for the whole period, this should be

reflected in a high degree of endemic species (Sadler, 1999). For the Nudibranchia, however, no endemic species have been identified. There is a theory that North Atlantic boreal faunas originated in a North Pacific center of origin prior to the formation of the Bering land bridge, about 3.5 million years ago, separating the Arctic Ocean from the North Pacific (Briggs, 2003). During subsequent glaciations the boreal fauna was displaced from the Arctic Ocean and a special arctic fauna evolved. There is no agreement about the presence and extent of ice cover during these periods (Barry, 1989), but presumably boreal species could not spread across the Arctic Ocean. No doubt, intertidal and shallow subtidal faunas were eliminated during periods of glaciation.

Other theories of origin for shallow marine faunas of oceanic islands include colonisation from the coast of the mainland, either directly or through "island-hopping" or "stepping stones". This seems to be the case for prosobranchs in tropical and warm temperate waters of the Atlantic Ocean (Leal and Bouchet, 1991). Successful colonisation depends on the distance to existing populations, prevailing currents, and duration of planktonic stages. Most nudibranchs have planktotrophic veliger larvae spending about 2-4 weeks in the plankton. Of the Faroese species only four have lecithotrophic development, and only *Cadlina laevis* has direct development (Thompson and Brown, 1984). Transportation can also be by rafting on floating objects, such as drifting seaweeds or pieces of wood or plastic. Transportation with fouling organisms on the hulls of ships is another possibility.

A total of 12 species from the Faroe Islands have amphiboreal-arctic distributions. These are also the most eurythermal, eurybathic and euryphagous species (Table 4; Thompson and Brown, 1984). *Dendronotus frondosus* may have dispersed from the North Pacific during inter-glacial periods and the Northeast Atlantic populations have separated from remaining populations subsequently. There are three species of *Dendronotus* in the Northeast Atlantic (Thollesson, 1998). Two of these occur also in the Northwest Atlantic. In the Northeast Pacific, on the other hand, there are 8 species, and in the Northwest Pacific there are two (Robillard, 1970; Behrens, 1991). Thus, there is little doubt that main speciation has occurred in the Northeast Pacific. The palaearctic *Dendronotus robustus (=D. velifer)* apparently does not occur south of Nordland county, Norway (Høisæter *et al.*, 2001), though it was recorded from Bohuslän (Skagerrack) by Odhner (1907). This record has been cited in several later publications (e.g. Lemche, 1938, 1941a,b; Platts, 1985). Odhner listed several specimens collected between 1889 and 1896, but the species has not been collected this far south since that time. *Acanthodoris pilosa* has a similarly wide distribution, and for the genus *Acanthodoris* there are also considerably more species in the Northeast Pacific (9 or 10) than in the Atlantic (one). The remaining species are from the southern hemisphere (one Atlantic and five Pacific) (Williams and Gosliner, 1979). For *Onchidoris bilamellata* and *O.*

muricata the global distributions are similar, but the genus *Onchidoris* has many more representatives in the North Atlantic Ocean (Thompson and Brown, 1984; Behrens, 1991) and thus this genus may have originated in the Atlantic rather than the Pacific. *Flabellina verrucosa, Cuthona nana* and *C. viridis* also have amphiboreal-arctic distributions. The number of species in both genera is high in the North Atlantic as well as the North Pacific, but few species have a broad amphiboreal-arctic distribution. Also, it appears that the most ancestral species of both genera have amphi-Atlantic-arctic distributions (Kuzirian, 1977; 1979; Millen, 1986; 1989). The wide distribution of a few species may indicate a fairly recent expansion of distributional ranges.

Cadlina laevis is one of the amphi-Atlantic species extending into the Mediterranean. The genus *Cadlina* is the temperate member of the colourful, tropical family Chromodorididae. Many species of *Cadlina* have a southern hemisphere distribution (Schrödl, 2000), and there are five species on the Pacific coast of North America (Behrens, 1991), one of which also occurs in the Northwest Atlantic (Bleakney, 1996). *Cadlina laevis* appears to be the only representative of the genus in the Northeast Atlantic, though the conspecificity with *C. glabra* from central Norway has been doubted (Thompson and Brown, 1984; Høisæter *et al.*, 2001). Only four of the 12 amphi-Atlantic species extend into arctic waters, whereas eight are found in the Mediterranean. Thus "island-hopping" is a more likely explanation of colonisation than a splitting up of an originally continuous distribution across the Arctic Ocean. Planktonic larvae can easily drift across the deep Faroe-Shetland Channel. Most of the amphi-Atlantic species are small hydroid feeders, which can also be introduced with hydroids fouling the hulls of ships.

Only two truly arctic species occur in the Faroe Islands. A further 12 species with boreal, mostly amphiboreal, distributions extend into arctic waters (Table 5). This is in contrast to the distribution of e.g. Terebellomorph polychaetes (Holthe, 1978), of which more than 50% of the species from the Faroe Islands have arctic distributions.

The largest zoogeographic group represented in the Faroe Islands is the species with Northeast Atlantic distributions (25 species). Ten of these species also occur in the Mediterranean, whereas only one extends into arctic waters. Many have their northern limit along the coast of Norway. *A. zetlandica* is a deep-water species with few records from depths of less than 100 m (Millen and Gosliner, 1985). This is confirmed by the BIOFAR material. Fourteen species of *Aldisa* are known, most of which occur in cold-temperate waters (Millen and Gosliner, 1985). Apparently the most ancestral ("primitive") species occur in the tropical Indo-West Pacific (Elwood *et al.*, 2000). About 12 nudibranch species have been considered endemic to central and northern Norway (Høisæter *et al.*, 2001). Four of these have now been recorded from the Faroe Islands, most of them from depths between 200 and 300 m. The distance from the Faroe Islands to Norway is about 675 km, whereas the distance to the

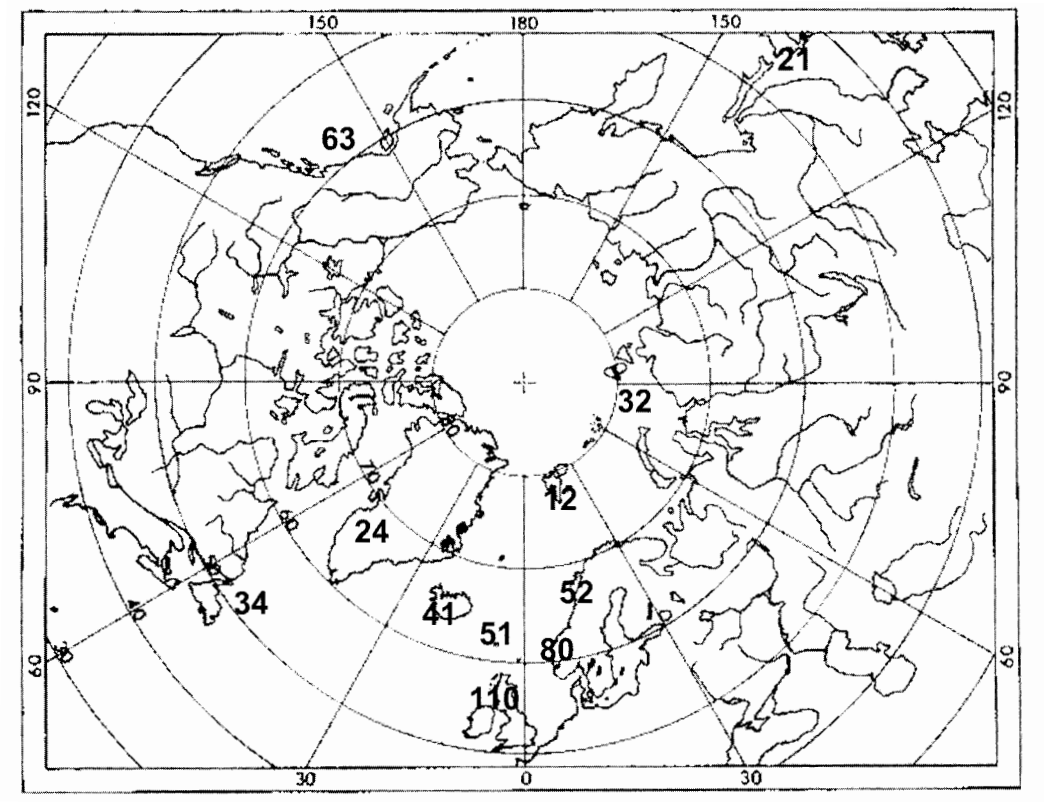

Figure 2. *Map of nudibranch species richness in northern boreal-arctic regions.*

Shetland Islands is only about 300 km. A slow current of 1 km/h would carry veligers from the Faroe Islands to Norway in 28 days, which is within the limits of planktonic life for most northern species. The warm North Atlantic Current passes through the Faroe-Shetland Channel towards the Norwegian coast, but there is no current in the opposite direction. Thus colonisation from the British Isles, either directly or via the Shetland Islands, seems to be the most likely. The occurrence of species found in central and northern Norway, but not in the British Isles, may indicate that distributions are continuous between the Faroe Islands and the coast of Norway along the rim of the Norwegian Sea basin, so that larvae only have to cross the Faroe-Shetland Channel. This might also explain why these species have not been found in southern Norway.

The nudibranch fauna of the Arctic Ocean is poorly studied. Old studies from Spitzbergen have described some species that have never been collected again. Also there are some Russian studies describing new species. As these descriptions are in Russian, it has not been possible to confirm

Table 6. *Zoogeographic affinities of nudibranch fauna of the Faroe Islands. The number of species found in the Faroe Islands is 51 (=N1). CJ= Jaccard's coefficient= 100(a/(N1+N2-a)). SD= Dice coefficient = 100(2a/(2a+b+c)). I=index of inclusion= 100(a/N_{min}). Ntot=total number of species from both locations; N2=number of species from location 2; a= number of shared species; b= number of species found only in location 1; c= number of species found only in location 2.*

Location2 (N2)	N tot	a	b	c	CJ	SD	I
British Isles (110)	119	42	9	68	35	52	82
S Norway (80)	87	44	7	36	51	65	86
N Norway (52)	65	37	15	15	56	71	73
Iceland (41)	62	30	21	11	48	65	73
Greenland (24)	57	18	33	6	32	48	75
E Canada (34)	63	22	29	12	35	52	65
Alaska (63)	105	9	42	54	8.6	16	18
Russian Arctic Seas (32)	68	15	36	17	22	36	47
Northern Japan (21)	67	5	46	16	7.5	14	24

their identity. The total number of species from arctic waters north of Russia and Siberia is 32. It has not been possible to identify distribution limits for these species, and hence this figure includes "western" species from the White Sea, Barents Sea and around Novaya Zemlya as well as "eastern" species from the Bering Strait, Chuckchin Sea and Laptev Sea. Only one truly arctic species has been found in the BIOFAR material. *Doridoxa ingolfiana* was found just north of the Faroe Islands at 603 m and 0°C. Both *D. ingolfiana* and *Cuthona abyssicola* also occur near Iceland and Greenland but have not been found near the coast of Norway.

There is a distinct latitudinal gradient in the number of nudibranch species, with 110 species occurring in the British Isles, 80 in southern Norway, 52 in northern Norway and only 12 in Spitzbergen (Figure 2). There is also a longitudinal gradient from east towards west, with 80 species in southern Norway, 51 in the Faroe Islands, 41 in Iceland and 24 in Greenland. Because so few species have been recorded from eastern Greenland, eastern and western Greenland have been lumped. Only five species have been recorded from Jan Mayen (Sneli and Steinnes, 1975; Gulliksen *et al.*, 2001) all of which also occur in eastern Greenland (Lemche, 1941a). The number of species increases on the east coast of Canada, where a few West Atlantic endemics occur and also a few North Pacific species have been recorded (Bleakney, 1996). The same trend is seen in the North Pacific with 63 species recorded from Alaska and northwestern Canada and only 21 species from northern Japan (Hokkaido).

The nudibranch fauna of the Faroe Islands shares the highest number of species with southern Norway (44) and the British Isles (42) and inclusion indices are over 80, meaning that 86% and 83% of the Faroese nudibranch fauna are included in those from southern Norway and the British Isles respectively. However, both coefficients of

similarities were higher for comparisons with northern Norway (Table 6). Only 73% were included in the fauna from northern Norway. Comparing the fauna of the British Isles and southern Norway showed slightly higher similarity (CJ=56; SD=72), whereas the British Isles compared with northern Norway showed lower similarity (CJ=32; SD=48). The similarity coefficients for southern Norway compared with northern Norway were: CJ=48 and SD=65. Inclusion indices were 85 for the fauna of southern Norway and the British Isles, 75 for the fauna of northern Norway and the British Isles, and 83 for the fauna of northern and southern Norway.

From the above results it can be concluded that the nudibranch fauna of the Faroe Islands may have different origins. A few species may be ancient invaders from the North Pacific, but most probably originated by colonisation from the British Isles. It seems that occasionally species with a more southerly distribution, e.g. *Lomanotus genei*, may reach as far north as the Faroe Islands, but so far have not reached the coast of Norway. On the other hand, arctic species, as *Doridoxa ingolfiana*, may also occasionally occur around the Faroe Islands. In this connection it should be noted that the occurrence of an extreme southerly species was in a different year from that of the arctic species. Shifting currents are probably important for the success or failure of settlement of these species. The single specimen of *L. genei* was very small and thus probably a recent settlement in July 1987, whereas the single specimen of *D. ingolfiana* was 12 mm long preserved, which is as big as the type specimen (until now the biggest specimen known) and thus may have been present for some time when it was collected in June 1989. The number of Northeast Atlantic species decreases from the Faroe Islands towards Iceland, Greenland and eastern Canada. Inclusion indices show that 73% of the nudibranch fauna from Iceland was included in the Faroese fauna, 75% of the Greenland fauna, but only 65% of the fauna of eastern Canada. Hence the “stepping-stone” or "island-hopping" hypothesis of colonisation cannot be rejected.

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