Helgol Mar Res (2004) 58: 289–302
DOI 10.1007/s10152-004-0194-2

ORIGINAL ARTICLE

Inka Bartsch · Ian Tittley

The rocky intertidal biotopes of Helgoland: present and past

Received: 1 April 2003 / Revised: 1 April 2004 / Accepted: 10 July 2004 / Published online: 6 November 2004

Abstract Nineteen of the 57 littoral rocky shore biotopes and 4 of the 26 variants as well as 1 sublittoral fringe biotope classified for Britain and Ireland have been recorded on Helgoland in this baseline study. Most of the wave-cut platform is at sublittoral and lower littoral levels and most high eulittoral biotopes are confined to narrow zones on seawalls. Large areas of gently sloping lower eulittoral and also boulder areas adjacent to seawalls are characterised by a mixture of two or more biotopes. Only 4 of the 23 littoral biotopes and variants are characterised by faunal species. Comparison with past descriptions of intertidal communities suggests continuing presence of most of the autochthonous biotopes over the past 80 years but also change due to the invasion of the macroalgae *Mastocarpus stellatus* and *Sargassum muticum* over the past 20 years. One previously recorded cave biotope and a sublittoral seagrass site have become extinct due to habitat loss while other biotopes probably have extended their range due to habitat increase. The presence of 4 intertidal biotopes (20%) considered rare or scarce in Britain supports the recognition of Helgoland as a site of special conservation in a regional and international context.

Keywords Littoral biotopes · Biodiversity change · Helgoland · Non-native species

Communicated by K. Wiltshire

I. Bartsch (✉)
Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27515 Bremerhaven, Germany
E-mail: ibartsch@awi-bremerhaven.de
Tel.: +49-471-48311404
Fax: +49-471-48311425

I. Tittley
Natural History Museum, London, SW7 5BD, UK

Introduction

A lack of integrated information for marine ecosystems, particularly knowledge of the composition and distribution of communities of plants and animals and associated habitats, is a hindrance both to scientific study and to the development of scientifically based policies for managing the resources of the coastal zone (Foster-Smith 2001). This applies to Helgoland and Dune despite intensive study of the islands' marine fauna and flora over the past 150 years (see Kuckuck 1894, 1897a, 1897b, 1897c; von Dalla Torre 1889; Caspers 1938; Ziegelmeier 1957, 1966; Kornmann and Sahling 1977, 1983, 1994; Gillandt 1979; Janke 1986, 1990; Reichert 2003).

Marine biotopes

The classification of marine biota as biotopes and their spatial recording, as with vegetation mapping on the land, was developed as a practical tool to assist conservation and site management of marine biodiversity, environmental impact assessment, monitoring management practices, and the prediction of possible future changes (Kent and Coker 1992; Connor et al. 1997a, 2003; Tittley et al. 1998). The underlying concept implies that a biotope in a particular area is an assemblage of species that may occur recurrently within a larger region (Kent and Coker 1992). Thus observation of the temporal and spatial dynamics of biotopes and/or biotope complexes via mapping and/or remote sensing will provide biodiversity information at a grosser scale or higher hierarchical level in an ecological classification than the species level. The ranked classification of ecological units as developed by Connor et al. (1997a, 1997b, 2003) indicates similarity by the position in the hierarchy. It also creates a basis for ecological comparison both within and between biogeographical regions (cf. Tittley and Neto 2000).

Previous studies of marine communities on Helgoland

Ecological studies that describe the marine communities of Helgoland and Dune are few and largely concern the algal vegetation; however, Janke (1986, 1990) and Reichert (2003) described in detail the intertidal fauna and dominant flora and their distribution on the northeast coast of Helgoland. Kuckuck (1897a) undertook the first description of the principal intertidal algal communities and presented a few photographs but most of his observations and photographs have been lost. Subsequently Nienburg (1930) defined the species assemblages on seawalls surrounding the red sandstone cliffs, the intertidal and subtidal red sandstone wave-cut platform, sublittoral stones and cobbles ("Geröllzone") on the seabed of the north harbour, and the chalk reefs of Dune Island. Schmidt (1928) undertook a similar study of the algal communities of the cliffs and wave-cut platforms and provided a few photographic records. Den Hartog's (1959) classification of the algal communities differed in its quantitative and phytosociological approach. SCUBA diving enabled Lüning (1970) to chart for the first time the vertical distribution of the sublittoral algal vegetation. Tittley (1982) undertook transect studies on the few remaining lengths of natural red sandstone cliff and also artificial seawalls and harbour walls. Brünger (1989) again used the phytosociological approach for intertidal communities, providing additional quantitative data. De Kluijver (1991) described sublittoral animal-dominated communities in detail.

Aims and objectives

The principal aim of this study was to identify the biotopes present on Helgoland (excluding Dune Island) using the British biotope classification and thereby to test its applicability. A second aim was to compare descriptive ecological data from past studies with data from the present survey to obtain a temporal perspective on the stability of the intertidal biotopes.

Methods

Present biotopes

Fieldwork was undertaken on seven occasions (12–24 July 1999, 13–23 June 2000, 16–24 June 2001, 25–29 April 2002, 10–13 September 2002, 10–16 March 2003, and 1–6 July 2003) to record the intertidal biotopes on Helgoland. Biotopes were identified using the approaches of Connor et al. (1997a, 1997b, 2003), Foster-Smith (2001), and Hiscock (1996). As neither map nor aerial photographs of the intertidal region were available during the fieldwork period of 1999 to 2002, the accessible intertidal region was characterised photographically and supported by topographical sketches. The boundaries of communities were outlined in the sketches. An approximate identification of communities was achieved by matching the visually abundant cover and underflora species with descriptions in Connor et al. (1997a). Species abundance data (percent cover of macrobenthos in 0.50×0.50 m quadrats) were taken at points in areas subjectively chosen to be representative for the respective biotopes or mixture of biotopes. The presupposed biotopes were sampled around the island and with $n \geq 5$. This generated a total of 182 quantitative quadrat points. The positions of sampling quadrats were recorded using a differential global positioning system (DGPS) with an accuracy of 1–7 m (ESYS GmbH, Berlin). Figure 1 shows the intertidal area and the names and locations of sites mentioned in the text. The quantitative data were iteratively compared with the biotope descriptions in Connor et al. (1997a, 2003). Seasonal variation was identified by recording the same sites in spring, summer, and autumn. This biotope survey presupposed a knowledge of the biota, and a clear, if subjective, impression of the types of community (see Kent and Coker 1992; Dierschke 1994). Habitat information including topography, substrate, relative wave exposure according to the prevailing winds and relative height on the shore was also noted throughout the study. Salinity is fully marine except at a few sites where there is freshwater run-off down the cliffs.

►

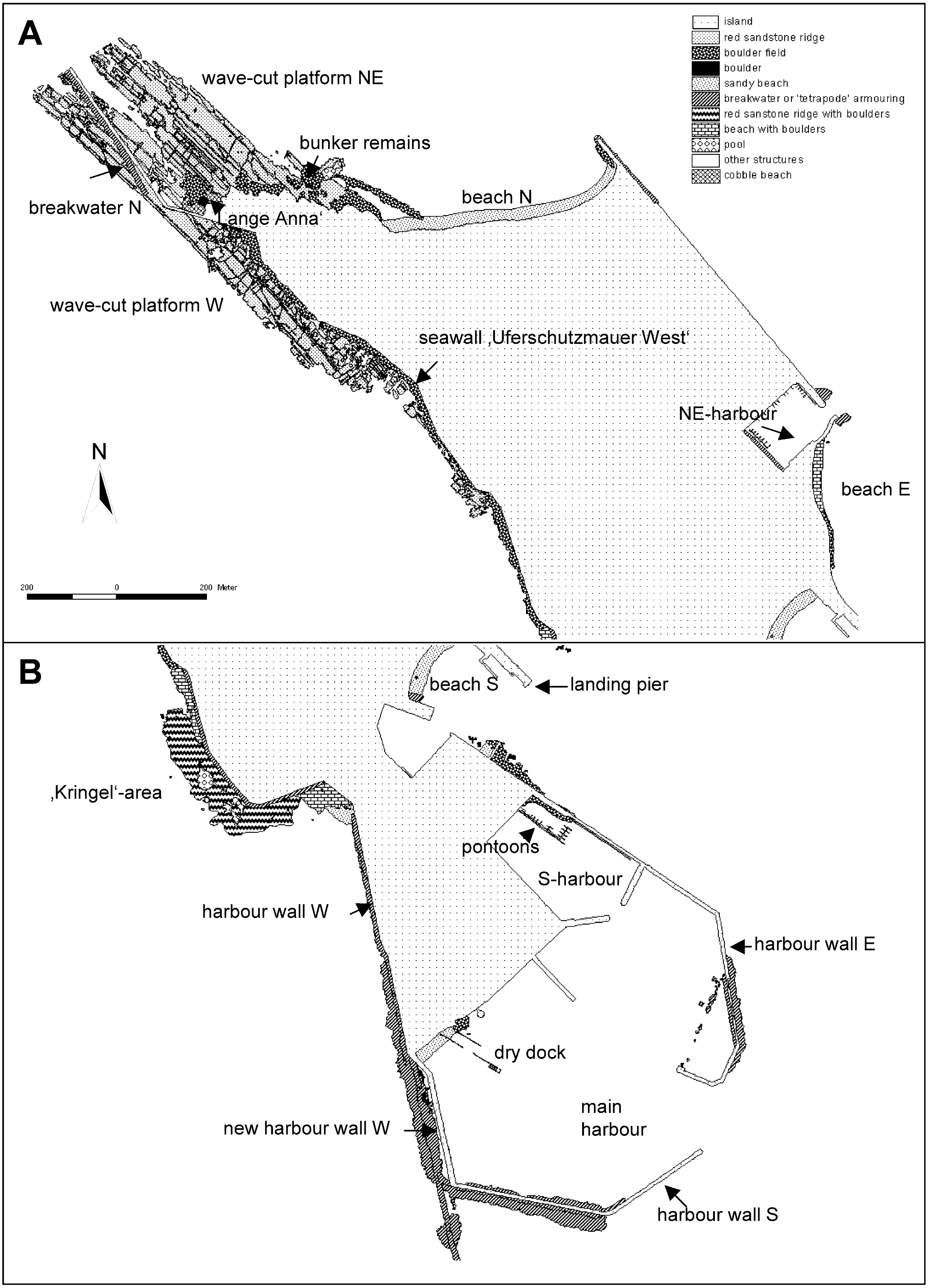
Fig. 1A, B Digitised map of Helgoland and its intertidal zone. **A** and **B** show a continuous map that is separated only for reasons of space

Site map

Figure 1 was created in 2003 on the basis of three georeferenced black-and-white orthophotographs provided by the Landesvermessungsamt Schleswig Holstein, Kiel, Germany at a scale of 1:7000 with a resolution of 0.4 m showing Helgoland and its intertidal region. The original photographs (Agfa Aviphot Pan 200) were taken on 26 May 2001 around low water. The digital orthophotographs were enlarged to a scale of 1:200 or 1:300 and all visible geomorphological structures were digitised and classified using ArcView 3.2 (ESRI, Germany). Colour field photographs supported this task. The slight mismatch of about 0.5 m at the transition zone between the orthophotographs was adjusted. As no digital elevation information was available, the outline of ridges was followed along lines of similar grey tones and thus is somewhat subjective.

The biotope classification for Britain and Ireland

Identification of biotopes in the British classification is through a hierarchy of ranked units or a matrix of information on habitats and species assemblages (Connor et al. 1997a, 2003). The primary divisions of the


A
island
red sandstone ridge
boulder field
boulder
sandy beach
breakwater or 'tetrapode' armouring
red sanstone ridge with boulders
beach with boulders
pool
other structures
cobble beach
wave-cut platform NE
bunker remains
breakwater N
'Lange Anna'
beach N
wave-cut platform W
seawall ,Uferschutzmauer West'
NE-harbour
beach E
N
200
0
200 Meter
B
beach S
landing pier
,Kringel'-area
pontoons
S-harbour
harbour wall W
harbour wall E
dry dock
main
harbour
new harbour wall W
harbour wall S

classification concern physical features, firstly rock or sediment substratum, secondly wave-exposure conditions, and thirdly shore level. The classification thus combines biological and physical features and in this way differs from the marine phytosociological approach of den Hartog (1959). The largest unit of biological feature is the 'biotope complex' and it contains one or more biotopes. Variants [also referred to by Connor et al. (1997a, 1997b) as sub-biotopes] describe variation types within a biotope. Rockpool, cave biotopes, and ephemeral biotopes are classified separately. Connor et al. (1997a, 2003) provide a full ecological description for each biotope complex, biotope, or variant in the classification; the characterising species and their abundance are given, and the associated species are listed. Each unit of the classification is given a code that indicates the physical and biological features present; information on the distribution and frequency of each biotope is also given.

Past biotopes

Past information on the ecology of the marine flora and fauna of Helgoland was collated and reviewed from the published literature. The ecological and community information given was interpreted to identify the principal intertidal communities according to the British biotope classification. This information was used to identify differences and/or similarities in intertidal biotopes of Helgoland with time.

Results

The biotopes and complexes recorded

The intertidal marine biotopes identified in the present survey are listed in Tables 1 and 2. The tables give an overview of the names, the codes adopted from Connor et al. (2003), the visually dominant species on Helgoland, the substrate, relative height on the shore, spatial occurrence, and the observed seasonality. The identification (ID) numbers are for easy comparison of biotopes between all three tables and the text. Of the 57 intertidal rock and cave biotopes itemised in Connor et al. (1997b, 2003) 19 have been recorded for Helgoland. Additionally, 4 variants described by Connor et al. (2003) and 1 sublittoral fringe biotope were also recorded and 1 new variant is proposed.

Habitat complex: features on eulittoral rock (lichens, caves, rockpools, and ephemeral seaweeds; FLR)

Biotope complex: lichens or small green algae on supralittoral rock (FLR.Lic) Four biotopes of this complex were well developed in the upper eulittoral and supralittoral on Helgoland. Although *Verrucaria* spp. formed discoid patches on erratic basalt blocks, the biotope FLR.Lic.Ver (see Connor et al. 2003) was not present.

FLR.Lic.YG (ID 1) The biotope characterised by 'yellow and grey lichens' occurred principally in the supralittoral on manmade structures but was not investigated in detail.

FLR.Lic.Pra (ID 2) The '*Prasiola stipitata* biotope' formed a thin adherent layer of small thalli at supralittoral levels on manmade and natural substrata near bird roosts; the biotope extended to spray-zone levels where the characterising species were *Rosenvingiella polyrhiza* (Rosenvinge) P.C. Silva and *P. calophylla* (Carmichael ex Greville) Kützing. It was best developed in spring. Extensive pure stands of *R. polyrhiza* occurred in March and July 2003 and further investigation is needed to verify a distinct '*Rosenvingiella*' biotope.

FLR.Lic.Bli (ID 3) The biotope characterised by *Blidingia* spp. was recorded commonly in summer as a distinct green band on natural and manmade substrata at mean high water level (MHW); in spring, by contrast, it was noted as a discontinuous band. It is especially well developed on concrete 'tetrapods' (coastal armouring) together with *Porphyra umbilicalis* (Linnaeus) Kützing but is rare on natural red sandstone. In March 2003 it was observed locally overgrowing a barnacle biotope.

FLR.Lic.UloUro (ID 4) The '*Ulothrix–Urospora* biotope' occurred abundantly in spring as an adherent layer of filaments on red sandstone rocks and boulders at upper mid-littoral shore levels below the biotopes characterised by *Blidingia* spp. and *Enteromorpha–Porphyra* spp. *Ulothrix* and *Urospora* spp. occasionally occurred among the latter and the biotope was not found in its expected position at eulittoral fringe levels above the '*Blidingia*-biotope'. In spring it formed a dark-green band in places discoloured by epiphytic diatoms while in summer it was replaced by dense stands of *Enteromorpha* spp.

Biotope complex: rockpools (FLR.Rkp) This habitat on Helgoland mostly comprised shallow channels that remained in direct contact with the sea during low tide. Three biotopes and one variant were commonly recorded on the wave-cut platform.

FLR.Rkp.G (ID 5) The 'green seaweeds (*Enteromorpha* spp. and *Cladophora* spp.) in shallow upper shore rockpools' biotope was recorded in limited extent on horizontal surfaces of harbour walls. The species content, seasonality, and spatial extent require further investigation.

FLR.Rkp.Cor (ID 6) '*Corallina* rockpools' were a common and characteristic feature of the wave-cut platform and showed seasonal facies. Those without

Table 1 The intertidal marine biotopes of Helgoland, visually dominant species. Biotope codes and names according to Connor et al. (1997b, 2003). The identification (*ID*) numbers enable easy comparison between tables and text. Author names of species are only added if not mentioned elsewhere in the text

ID	Biotope code Version 03.02	Biotope name	Visually dominant species at Helgoland
1	FLR.Lic.YG	'Yellow and grey lichens on supralittoral rock'	Species composition needs further investigation
2	FLR.Lic.Pra	'*Prasiola stipitata* on nitrate-enriched supralittoral or littoral fringe rock'	*P. stipitata* Suhr ex Jessen
3	FLR.Lic.Bli	'*Blidingia* spp. on vertical littoral fringe soft rock'	*B. minima* (Nägeli ex Kützing) Kylin, *B. marginata* (J. Agardh) P.J.L. Dangeard ex Bliding, *Porphyra umbilicalis*
4	FLR.Lic.UloUro	'*Ulothrix flacca* and *Urospora* spp. on freshwater-influenced vertical littoral fringe soft rock'	*Ulothrix* spp., *Urospora penicilliformis* (Roth) Areschoug, *Bangia atropurpurea*
5	FLR.Rkp.G[a]	'Green seaweeds (*Enteromorpha* spp. and *Cladophora* spp.) in shallow upper shore rockpools'	Species composition needs further investigation
6	FLR.Rkp.Cor	'*Corallina officinalis*, coralline crusts and brown seaweeds in shallow eulittoral rockpools'	*C. officinalis*, *Chondrus crispus*, crustose Corallinaceae, *Mastocarpus stellatus*, varying amounts of seasonal species (e.g. *Rhizoclonium tortuosum*, *Cladophora* spp., *Dumontia contorta*) *Fucus serratus* sparse
7	FLR.Rkp.FK	'Fucoids and kelps in deep eulittoral rockpools'	*F. serratus*, *Laminaria digitata*, *C. officinalis*, *Halidrys siliquosa*, crustose Corallinaceae
7.1	FLR.Rkp.FK.Sar	'*Sargassum muticum* in eulittoral rockpools'	*S. muticum*; *F. serratus* and/or *L. digitata* may be present in low quantities; underflora of *C. officinalis*, crustose Corallinaceae, *C. crispus*, *Cladophora* spp.
8.1	FLR.CvOv.SpR[a]	'Sponges and shade-tolerant red seaweeds on overhanging lower eulittoral bedrock and in cave entrances'	*Ceramium* spp., *Halichondria panicea* Pallas, others to be identified
9	FLR.Eph.Ent	'*Enteromorpha* spp. on freshwater-influenced and/or unstable upper eulittoral rock'	*E. intestinalis*
10	FLR.Eph.EntPor	'*Porphyra purpurea* and *Enteromorpha* spp. on sand-scoured mid or lower eulittoral rock'	*Enteromorpha* spp., *P. purpurea* (Roth) C. Agardh, *P. dioica* J. Brodie et L. M. Irvine; lower on shore including *Ulva lactuca*
11.1	HLR.Mus B.Sem.Sem	'*Semibalanus balanoides*, *Patella vulgata* and *Littorina* spp. on exposed to moderately exposed or vertical sheltered eulittoral rock'	Varying amount of *Semibalanus balanoides* and *Elminius modestus*, small gastropods, no *Patella* sp.; may be overgrown by *Blidingia* sp. during summer
11.2	HLR.Mus B.Sem.LitX	'*Semibalanus balanoides* and *Littorina* spp. on exposed to moderately exposed eulittoral boulders and cobbles'	High densities of *Littorina* spp., variable and patchy amount of *S. balanoides* and *E. modestus*, sparse *M. stellatus*
12	HLR.FR.Mas	'*Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock'	On exposed shores or harbour walls pure *M. stellatus*; otherwise mixture of *M. stellatus* and *C. crispus*; at more sheltered sublittoral fringe level dominant *C. crispus*
13	MLR.Mus F.MytFves	'*Mytilus edulis* and *Fucus vesiculosus* on moderately exposed mid eulittoral rock'	Patchy *M. edulis; Littorina* spp., low amount of *F. vesiculosus* and *M. stellatus*; *M. edulis* covered with brown crusts (e.g. *Ralfsia verrucosa*)
14	MLR.Mus F.MytFR	'*Mytilus edulis*, *Fucus serratus* and red seaweeds on moderately exposed lower eulittoral rock'	Patchy *M. edulis*, *Littorina* spp., low amounts of *F. serratus*, *C. crispus* and *M. stellatus; M. edulis*covered with brown crusts (e.g. *R. verrucosa*)
15	MLR.BF.FspiB	'*Fucus spiralis* on full salinity exposed to moderately exposed upper eulittoral rock'	*F. spiralis*, barnacles
16	MLR.BF.Fser	'Dense *Fucus serratus* on moderately exposed to very sheltered full salinity lower eulittoral rock'	Dense *F. serratus* visually dominant with underflora of *Cladophora rupestris*, *C. crispus*, *Phymatholithon lenormandii* (Areschoug) W. H. Adey, crustose Corallinaceae, *C. officinalis*
16.1	MLR.BF.Fser.R	'*Fucus serratus* and red seaweeds on moderately exposed lower eulittoral rock'	Mosaic of *F. serratus* with especially *C. crispus* and *M. stellatus*; additional seasonal species
17	MLR.BF.Rho	'*Rhodothamniella floridula* on sand-scoured lower eulittoral rock'	Obvious cover of *Ulva lactuca* producing a 'green aspect', *R. floridula* binding sand, *Codium fragile*, *C. crispus*, *Cladostephus spongiosus* (Hudson) C. Agardh; sparse varying amount of seasonal green algae(*Cladophora* spp., *Acrosiphonia* spp., *Enteromorpha* spp.)
18	LLR.F.Fves	'*Fucus vesiculosus* on full salinity moderately exposed to sheltered mid eulittoral rock'	*F. vesiculosus*, barnacles, varying amount of *M. stellatus*
19	LLR.F.Asc	'*Ascophyllum nodosum* on very sheltered mid eulittoral rock'	*A. nodosum*
20	MIR.KR.Ldig	'*Laminaria digitata* on moderately exposed sublittoral fringe rock'	Dense *L. digitata*, crustose Corallinaceae

[a] Present only in small patches

Table 2 The intertidal marine biotopes of Helgoland, habitat and occurrence (see Fig. 1 for locations). Biotope codes according to Connor et al. (1997b, 2003). *SupraL* Supralittoral; *UpEU*, *MidEu*, *Low Eu* upper, middle, and lower eulittoral; *LittF* littoral fringe; *SublF* sublittoral fringe; *con* concrete; *rs* red sandstone; *gra* granite

ID	Biotope code Version 03.02	Shore level	Substrate	Topography	Spatial extent and occurrence	Seasonality and remarks
1	FLR.Lic.YG	SupraL	Con	Harbour walls; breakwaters	Spatial extent unknown; patchy; present on many harbour walls	Unknown
2	FLR.Lic.Pra	SupraL	Con; bricks	Horizontal and vertical faces of harbour walls and breakwaters	Small to large patches; e.g. Lange Anna N-facing foot; top of harbour walls with bird roost	Varying in size over season; least developed in summer
3	FLR.Lic.Bli	LittF	Rs; con	Vertical faces of harbour or seawalls and breakwaters; vertical cliffs	Patches or compressed zone; present all around the island; esp. well developed on breakwaters at the 'Kringel'; may be found on top of HLR.MusB.Sem.Sem	Best developed in spring to summer
4	FLR.Lic.UloUro	UpEu to LittF	Rs; con	Boulder fields and vertical faces of seawalls	May occupy large areas on boulder zone by the wave-cut platform NE; otherwise compressed zone on seawalls or harbour walls	Only distinct in winter to spring; in other seasons very patchy or absent
5	FLR.Rkp.G	SupraL	Con	Horizontal faces on top of harbour walls	Unknown, but on broken platform of outer harbour wall E as single small pools	Unknown
6	FLR.Rkp.Cor	SublF	Rs	Shallow channels or sea-connected pools within wave-cut platform	Pure aspect sparse; often merging with FLR.Rkp.FK.Sar; commonly found within wave-cut platforms NE and W between *Fucus* ridges	Best recognised in winter with out seasonal summer species; appearance changes consider ably between winter and summer
7	FLR.Rkp.FK	SublF	Rs	Deep bomb craters and channels transversing wave-cut platform	Locally present in deep channels and bomb craters of wave-cut platform W; merging with FLR.Rkp.FK.Sar or MIR.KR.Ldig	Summer growth of *Sargassum* changes aspect into FLR.Rkp.FK.Sar
7.1	FLR.Rkp.FK.Sar	SublF	Rs	Shallow and deeper channels transversing wave-cut platform	Shallow and deep channels in the wave-cut platforms W and NE; largest intertidal standing channels east of breakwater N	Summer variant of FLR.Rkp.FK or FLR.Rkp.Cor
8.1	FLR.CvOv.SpR	LowEu to SublF	Rs	Vertical shaded faces of wave-cut platform ridges	Small patches present along *Fucus serratus* covered ridges meeting deep channels, e.g. on wave-cut platform W	Unknown
9	FLR.Eph.Ent	SupraL to UpEu	Rs	Vertical faces of cliffs or horizontal faces of platform	Rare; vertical cliff by wave-cut platform NE with freshwater run-off; detritus-disturbed platform areas east of 'Lange Anna'	Unknown
10	FLR.Eph.EntPor	Mid to low Eu	Rs; gra; con	Disturbed boulders; sites influenced by heavy siltation	May occupy whole boulder zone by the wave-cut platform NE; otherwise patchy, e.g. main harbour/dry dock, beach E and S	Typical biotope with *Porphyra* and *Enteromorpha* spp. best developed in spring and summer; otherwise patchy
11.1	HLR.MusB.Sem.Sem	UpEu	Con; gra	Sheltered to exposed vertical faces of harbour or seawalls	Unknown; e.g. broad band of 1-m widths along vertical faces of breakwater N	Overgrown by *Blidingia*spp. in summer
11.2	HLR.MusB.Sem.LitX	MidEu	Rs	Exposed unstable wave-cut platform	Covering a broad girdle at the 'Kringel'	Unknown
12	HLR.FR.Mas	MidEu to SublF	Rs; gra; con; basalt	Wave-cut platform (pure *Chondrus* or mixed *Chondrus*/*Mastocarpus* variant); exposed to moderately exposed hard substrate boulders and exposed sea and harbour walls (pure *Mastocarpus* variant)	Locally present on exposed seawalls or boulders (*Mastocarpus* variant), shallow ridge near bunker remains on the wave-cut platform NE (*Chondrus* variant), inner ridges of wave- cut platform W (mixed *Chondrus*/*Mastocarpus* variant)	Variable amount of *Fucus serratus* present; biotope may merge with MLR.BF.Fser.R; seasonal red and green algae may change aspect
13	MLR.MusF.MytFves	MidEu	Rs	Moderately exposed higher ridges of wave-cut platform	Large but patchy area on wave-cut platform NE that is transversed by channels with Rkp biotopes	No seasonal change except abundance of *Mytilus* and fucoids

14	MLR.MusF.MytFR	LowEU	Rs	Moderately exposed higher ridges of wave-cut platform	Large but patchy area on wave-cut platform NE that is transversed by channels with Rkp biotopes	No seasonal change except abundance of *Mytilus* and fucoids
15	MLR.BF.FspiB	UpEu	Rs; gra; con	Vertical faces of seawalls or harbour walls, breakwaters and boulders; on natural cliffs	Patchy or small compressed zone on vertical faces all around the island	Unknown
16	MLR.BF.Fser	LowEu	Rs	Wave-cut platform; boulders	Occupies extensive low-lying areas of the wave-cut platform NE and W; S harbour	Presence of seasonal species does not considerably alter visual aspect
16.1	MLR.BF.Fser.R	Mid to lowEu	Rs; gra; con; basalt	Boulders and wave-cut platform	Patches on ridges of wave-cut platform W adjacent to MLR.BF.Fser; broad band on hard substrate boulder fields in the wave-cut platforms NE and W adjacent to seawalls; pure biotope rare; on boulders often merging with other fucoid or green algal biotopes	Variable amount of red algae and fucoids; summer flush of green algae
17	MLR.BF.Rho	LowEu	Rs	Silted seaward facing ridges of wave-cut platform with a west to east slope	Very distinct; extent limited, but regularly present on wave-cut platform W and NE on *Fucus serratus*-free sites within MLR.BF.Fser and MLR.BF.Fser.R	Covered with variable amount of *Ulva lactuca* creating 'green aspect'
18	LLR.F.Fves	MidEu	Rs; gra; con	Boulders; wave-cut platform	Patchy; at no site forming a dense continuous band or area; pure biotope rare; merging with other fucoid biotopes on boulder fields adjacent to seawalls	Best developed at bunker remains and boulder field east of 'Lange Anna'
19	LLR.F.Asc	MidEu	Con; gra; only hard sub strate	Very sheltered harbour walls or boulders and wave-protected sites of breakwaters or boulders	Distinct zone on vertical faces or boulders with a continuous gradient; few sites, limited in extent; S harbour; protected sites along breakwater N; breakwater seaward of new harbour wall W	Unknown
20	MIR.KR.Ldig	SublF	Rs	Wave-cut platform	Extensive beds all around the island at sublittoral fringe level; partly merging with MLR.BF.Fser	Unknown

seasonal epiphytes occurred in late winter when *C. officinalis* Linnaeus had not died back due to frost. In spring *C. officinalis* was commonly overgrown by *Monostroma grevillei* (Thuret) Wittrock (March to May) and *Dumontia contorta* (S.G. Gmelin) Ruprecht (March to June/July). In summer, in shallow channels of the northeastern coast, this biotope was characterised by blanketing growths of *Rhizoclonium tortuosum* (Dillwyn) Kützing. On the west coast, seasonal species such as *Dictyota dichotoma* (Hudson) J.V. Lamouroux, *Leathesia difformis* (Linnaeus) Areschoug, *Cladophora* spp., and *Acrosiphonia* spp. occurred among or epiphytically on *C. officinalis*.

FLR.Rkp.FK (ID 7) and FLR.Rkp.FK.Sar (ID 7.1) Deeper channels between the sandstone ridges or bomb craters contained species that characterised the 'fucoids and kelp in deep eulittoral rockpools' biotope. A variant characterised by the invasive *Sargassum muticum* (Yendo) Fensholt was recorded in summer when *S. muticum* formed a blanketing layer in channels and lagoons. *S. muticum* died back in autumn to winter and was present only as small plants in spring. This variant intergraded with the 'fucoid and kelp' and '*Corallina*' biotopes. At other sites *Halidrys siliquosa* (Linnaeus) Lyngbye was the dominant species. Dense *Sargassum* cover in summer was also observed sporadically in shallow channels with shingle and sand that lie to the east of the northern breakwater (Fig. 1). This substrate and additional flora may suggest a 'seaweeds in sediment-floored eulittoral rockpools' biotope (FLR.Rkp.SwSed). The distinction between this and the *S. muticum* variant (LR.Fkp.FK.Sar) was not apparent to us.

Biotope complex: littoral caves and overhangs (FLR.CvOv) This complex was represented by a single cave in cliffs on the northeast coast and by overhangs associated with ridges ('Schichthöhlen') on the wave-cut platform. The cave was not investigated due to danger of cliff fall.

FLR.CvOv.SpR (ID 8.1) The 'sponges and shade-tolerant red seaweeds' biotope was recorded at lower eulittoral levels where ridges covered by *Fucus serratus* Linnaeus were cut by deep channels. This biotope was patchily present and of limited extent and was not further investigated.

Biotope complex: ephemeral green or red seaweeds (freshwater or sand-influenced; FLR.Eph) Two biotopes of this complex were frequently recorded around the island.

FLR.Eph.Ent (ID 9) Large *Enteromorpha intestinalis* (Linnaeus) Link patches were present in one place at the north end of the island and formed a distinct biotope on the cliff face where there was freshwater seepage. *E. intestinalis* was otherwise present as part of the FLR.Eph.EntPor biotope (see below).

FLR.Eph.EntPor (ID 10) The '*Porphyra purpurea* and *Enteromorpha* biotope' occurred abundantly and extensively in summer on substrata that were characterised by physical disturbance such as sand scour, erosion, and detritus deposits. It showed clear seasonal changes; in late autumn to winter it died back completely (Janke 1986; Bartsch, personal observation) while in spring it was discontinuously present over large areas. Species composition in the biotope varied from *Enteromorpha* spp. and *Porphyra* spp. co-dominance to almost pure growths of one or the other.

Habitat complex: high energy eulittoral rock (HLR)

Biotope complex: Mytilus edulis, barnacles and Patella spp. on exposed to moderately exposed, or vertical sheltered eulittoral rock (HLR.MusB) This biotope complex was only represented on Helgoland by a single biotope with its two variants.

HLR.MusB.Sem.Sem (ID 11.1) The biotope occurred on wave-exposed harbour walls and contained a varying abundance of *Semibalanus balanoides* Linnaeus and *Elminius modestus* Darwin. A common species of the biotope in Britain, the limpet *Patella vulgata* Linnaeus, occurs only rarely on Helgoland (Götting 2001). Thus the biotope is characterised by a dense barnacle cover.

HLR.MusB.Sem.LitX (ID 11.2) '*Semibalanus balanoides* and *Littorina* spp. on exposed to moderately exposed eulittoral boulders and cobbles' occupied large areas in wave-exposed conditions at the southwest corner of the island ('Kringel') where mobile red sandstone cobbles formed an unstable surface over horizontally fractured bedrock. The biotope differed from that described in Connor et al. (2003) in containing sparse *Mastocarpus stellatus* (Stackhouse) Guiry and lacking fucoids.

Biotope complex: robust fucoids and/or red seaweeds (HLR.FR) This biotope complex was represented on Helgoland by a single biotope.

HLR.FR.Mas (ID 12) The '*Mastocarpus* and *Chondrus*' biotope occurred commonly on exposed to moderately exposed sites on manmade and natural substrata at mid to low eulittoral levels where *Mastocarpus* was predominant and on flat red sandstone sites at sublittoral fringe levels where *Chondrus* was predominant. In these situations the biotope did not cover extensive areas and often formed a transition with a *Fucus serratus* and red algal mosaic (MLR.BF.Fser.R, ID 16.1 see below). On the west coast of Helgoland the two grew together on the wave-cut platform and formed patchy mats. Pure stands of *M. stellatus* were commonly recorded at wave-exposed sites on manmade boulders, concrete tetrapods, or vertical harbour walls. Dense *C. crispus* Stackhouse occurred by contrast rarely, at lowest eulittoral levels in the northeast near the bunker remains

(Fig. 1). In late winter, summer seasonal species such as *Dumontia contorta* and *Rhizoclonium tortuosum* that often masked the *Chondrus*/*Mastocarpus* association were absent. The distinction between HLR.FR.Mas and MLR.BF.Fser.R was not always clear.

Habitat complex: moderate energy eulittoral rock (MLR)

Biotope complex: mussels and fucoids on moderately exposed shores (MLR.MusF) This complex on Helgoland comprised two biotopes.

MLR.MusF.MytFves (ID 13) and MLR.MusF.MytFR (ID 14) The '*Mytilus edulis* and *Fucus vesiculosus*' and '*Mytilus edulis*, *Fucus serratus* and red seaweeds' biotopes were both restricted to the mid-eulittoral zone of the northeastern wave-cut platform. Although they were only patchily present, they occupied large areas and overlapped extensively.

Biotope complex: barnacles and fucoids on moderately exposed shores (MLR.BF) Three biotopes and one variant were recorded for Helgoland, two of which covered extensive areas of the wave-cut platform.

MLR.BF.FspiB (ID 15) Although *Fucus spiralis* Linnaeus is a common species on the island, it occurred mainly as a narrow linear band on seawalls. *F. spiralis* was more extensively present in only a few places such as the sheltered sides of harbour walls and on the bunker remains on the northeast coast.

MLR.BF.Fser (ID 16) and MLR.BF.Fser.R (ID 16.1) The '*Fucus serratus*' biotope was extensively present on the wave-cut platform at lower eulittoral levels on the northeast and west coasts. At mid-eulittoral levels in the west, a dense *F. serratus* canopy was replaced by the 'robust red algae' *Mastocarpus stellatus* and *Chondrus crispus* (see Connor et al. 2003) and formed a continuum with the '*Fucus serratus* and red seaweeds' variant (MLR.BF.Fser.R). *F. serratus* also extensively overlapped with *Laminaria digitata* (Hudson) J.V. Lamouroux to form a mixed canopy on gently sloping lower eulittoral rock. On jumbled boulders at upper eulittoral levels in front of the seawall on the west coast ('Uferschutzmauer') *F. serratus* grew together with *F. vesiculosus* Linnaeus and *F. spiralis* to form a 'mixed fucoid' canopy that also contained *M. stellatus* and *C. crispus*.

MLR.BF.Rho (ID 17) The cushion-forming '*Rhodothamniella floridula*' biotope occurred on the upper surfaces of seaward-facing lower eulittoral ridges. *R. floridula* (Dillwyn) Feldmann commonly binds silt to form cushion-like growths. In summer it was often overgrown by *Acrosiphonia* spp., *Cladophora* spp., *Enteromorpha* spp., and *Ulva lactuca* Linnaeus, creating a green aspect. In other areas where silt was bound by vegetation *R. floridula* was absent and the biotope was characterised by green algae and small amounts of *Chondrus crispus*. *Codium fragile* (Suringar) Hariot was an indicator species for this biotope although only occasionally present.

Habitat complex: low-energy eulittoral rock (fucoid shores; LLR)

Biotope complex: dense fucoids on sheltered littoral fringe and littoral rock (LLR.F) Three biotopes of this complex were recorded on Helgoland but were only locally present and of limited extent. In general, this biotope complex was restricted to harbours, protected inner harbour walls, and protected sites on the northeastern wave-cut platform.

LLR.F.Fves (ID 18) *Fucus vesiculosus* formed a biotope of limited extent on the northeast coast although individual plants occurred around the island.

LLR.F.Asc (ID 19) *Ascophyllum nodosum* (Linnaeus) Le Jolis was recorded on the north, south, and east harbour seawalls, on boulders and concrete tetrapods not directly exposed to wave action; it only formed beds of some horizontal extent on the boulder field in the sheltered south harbour. The obligate epiphyte *Vertebrata lanosa* (Linnaeus) T.A. Christensen (sensu Choi et al. 2001) was rarely present.

Habitat complex: moderately exposed infralittoral rock (MIR)

Biotope complex: kelp and red seaweeds (moderately exposed rock; MIR.KR) MIR.KR.Ldig (ID 20) A canopy of *Laminaria digitata* at sublittoral fringe levels was an extensive and obvious feature around much of the island on both natural and manmade substrata.

Comparison with previously described communities

Table 3 lists the intertidal communities described during the past 100 years and compares them with the biotopes recorded in the present study. Twelve biotopes that have been regularly recorded in the past 80–100 years still occupy much of the intertidal area. Two biotopes (cave community; *Zostera marina* Linnaeus field) were not recently recorded and a further two (*Ralfsia* association; *Bangia* association) cf. Nienburg 1930) could not be matched against the descriptions of Connor et al. (2003). The '*Mytilus* with *Fucus* biotopes' detected in the present survey were not recorded previously. Two biotopes not recorded previously (FLR.Rkp.FK.Sar and

Table 3 The intertidal marine biotopes of Helgoland, comparison of biotope equivalents previously described with current situation. Biotope codes according to Connor et al. (1997b, 2003).*NP* biotopes not present on Helgoland at this time

ID	Biotope code Version 03.02	1894/1897[Ku]	1928[Sch]	1930[Ni]	1959[DH]	1970[L]	1977[KS]	1982[MM]	1986/1990[J]	1989[Br]	1994[KS]	1999–2003
1	FLR.Lic.YG								X			X
2	FLR.Lic.Pra						X		X	X		X
no ID	*Ralfsia* association	*Ralfsia*-band	*Ralfsia*-band	X		*Ralfsia*-band	NP	NP	NP	NP	NP	NP
3	FLR.Lic.Bli		X		X		X	X	1990, Fig. 15	X		X
no ID	*Bangia* association		*Calothrix* *Bangia*	Fig. 25a	X	X		*Bangia*		*Bangia*		
4	FLR.Lic.UloUro		X			X	Fig 1a	X		Fig. 4		X
5	FLR.Rkp.G		X				X					X
6	FLR.Rkp.Cor		X	X				X	X	Fig. 13		X
7	FLR.Rkp.FK			Fig. 30b				X	X			X
7.1	FLR.Rkp.FK.Sar	NP	NP	NP	NP	NP	NP	NP	NP	NP	X	X
no ID	Cave community	X							Janke pers. comm.	NP	NP	NP
8.1	FLR.CvOv.SpR								X			X
9	FLR.Eph.Ent		X	Fig. 25a						X		X
10	FLR.Eph.EntPor		X		X			X	1990, Fig. 4	X		X
11.1	HLR.MusB.Sem.Sem		X						X			X
11.2	HLR.MusB.Sem.LitX	NP	NP	NP					X			X
12	HLR.FR.Mas							X	X		X	X
13	MLR.MusF.MytFves	NP	NP	NP	NP	NP	NP	NP	1990, Fig. 6	X		X
14	MLR.MusF.MytFR	NP	NP	NP	NP	NP	NP	NP	X	X		X
15	MLR.BF.FspiB	X	X	Fig. 25a	X	X	X	X	1990, Fig. 15	X		X
16	MLR.BF.Fser	1894, Fig. XIII	X	X	X	X	X	X	1990, Fig. 7	Fig. 8		X
16.1	MLR.BF.Fser.R			Fig. 30a								X
17	MLR.BF.Rho		X	Fig. 29b	X	X	Fig. 91a	X				X
18	LLR.F.Fves	X	X	Fig. 26a	X	X	X	X	X			X
19	LLR.F.Asc	X	X	Fig. 27a		X	X		X	X		X
20	MIR.KR.Ldig	X	X	Fig. 27b	X	X	X	X	1990, Fig. 11	Fig. 12		X
no ID	Sublittoral *Zostera marina* field	X	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP

Br Brünger (1989); *DH* den Hartog (1959); *J* Janke (1986, 1990); *Ni* Nienburg (1930); *Ku* Kuckuck (1894, 1897a); *KS* Kornmann and Sahling (1977, 1994); *L* Lange (1970); *MM* Munda and Markham (1982); *Sch* Schmidt (1928)

HLR.FR.Mas) are due to the arrival of non-native species (*Sargassum muticum* and *Mastocarpus stellatus*).

Discussion

Identification and classification of biotopes

The results of the study show that the intertidal rocky shore marine biota of Helgoland formed species assemblages that largely concurred with the descriptions of biotopes in the classification for Britain and Ireland. (See Tables 1, 2). Although Helgoland is located 500 km east of Great Britain, it lies within a biogeographical region of the northern North Atlantic Ocean where the intertidal biota on moderately wave-exposed and sheltered rocky shores are characterised by large canopy-forming brown algae, and on wave-exposed shores by barnacles and mussels.

The range of habitats on Helgoland is limited by its small size, thus only a third of the intertidal rocky shore biotopes of Britain are present (19 out of 57 biotopes in Britain). Those of sheltered to very sheltered conditions such as the *Ascophyllum nodosum* biotope (LLR.F.Asc ID 19) are few and would not exist but for the construction of harbours. The addition of manmade habitats to the island has resulted in an increase in diversity of habitats and communities. The absence in Helgoland of other biotopes present in Britain may be explained by species distribution ranges not reaching the islands, or their ecophysiology not tolerating the environmental conditions of Helgoland (South and Tittley 1986; Lüning 1990; Rueness et al. 1997). The occurrence and distribution of intertidal biotopes is also influenced by the geomorphology of Helgoland where upper eulittoral levels are vertical and limited in extent and lower eulittoral levels are extensive. Rockpool biotopes are therefore largely absent at upper eulittoral levels.

The recognition of biotopes on Helgoland was not always straightforward. On vertical faces the biotopes were often compressed to narrow zones and thus did not fit the spatial requirement of Connor et al. (1997a, 2003) that for mapping, a biotope should occupy an area larger than 25 m^2. The distinction between biotopes on the wave-cut platform was unclear where the change in the determining environmental factors was either gradual or variable, as in the boulder fields. *Fucus serratus* and *Laminaria digitata* grew together over large areas of the wave-cut platform and formed a continuum from pure *F. serratus* stands (MLR.BF.Fser ID 16) at low eulittoral levels to pure *L. digitata* stands (MIR.KR.Ldig ID 20) at sublittoral fringe levels. Similarly, *F. serratus*, *F. vesiculosus*, and *F. spiralis* grew together in the narrow boulder zone adjacent to seawalls and harbour walls as already described by Munda and Kremer (1997). This created an overlap of biotopes (MLR.BF.FspiB ID 15, LLR.F.Fves ID 18, and MLR.BF.Fser ID 16) and supports the opposing view to community classification. Furthermore it presented a problem with assignment of the biota recorded in the field to a biotope. A pragmatic solution for mapping purposes will be to treat extensive areas of overlapping biotopes as distinct units designated 'mixed biotopes'.

Another difficulty in assigning field observations to the described biotopes or their variants arose in cases where a single dominant species was involved, as in sites dominated by *F. serratus*. We identified areas abundantly covered by *F. serratus* as MLR.BF.Fser according to Connor et al. (1997a, 2003) due to the presence of crustose Corallinaceae, *Chondrus crispus*, and *Corallina officinalis*. The sheltered biotope LLR.F.Fserr.FS is characterised by a 'dense canopy of the wrack *Fucus serratus*' and contained *Cladophora rupestris* (Linnaeus) Kützing (Connor et al. 2003), a frequent constituent of the Helgoland *F. serratus* biotope. This suggests an intermediate situation and presented a difficulty in their recognition and separation. Further work on defining identifier species or improved abundance cut-off levels have to be developed in order to recognise two biotopes satisfactorily.

A sound biotope classification requires the analysis of many empirical data sets and the use of numerical analytical methods to help achieve this (Connor et al. 1997a). The present evaluation of Helgoland marine biotopes was based on comparing observed field situations with the biotope definitions of Connor et al. (1997a, 1997b, 2003). Our next step is to attempt to confirm the existence of biotopes using an alternative approach that relies on numerical analysis of quantitative field data. The subjective, descriptive approach is commonly used for the completion of coastal biodiversity surveys within a reasonable time and cost frame (Kent and Coker 1992; Foster-Smith 2001; John et al. 2002). Even in such rapid inventory-type surveys we recommend validation data such as basic habitat details, main cover species, and their abundance (as in Table 2) be collected to match against future changes of the classification.

Present and past occurrence of marine biotopes

The comparison of present and past marine biotopes (Table 3) identified both change and stability in the biotopes present on Helgoland; temporal comparison of biotopes presents another approach for recording change in biodiversity. The main changes recorded here have been caused by habitat loss and alteration (e.g. construction of seawalls and harbours) and extensive colonisation by non-native species.

The natural spread of *Ascophyllum nodosum* soon after the construction of the west seawall ('Uferschutzmauer') and the main harbour in the early twentieth century (Nienburg 1930) led to the formation of a biotope new to Helgoland although single attached plants of *A. nodosum* had been collected by Kuckuck on erratic basalt blocs at the west coast (Nienburg 1930; Bartsch and Kuhlenkamp 2000; specimens in the Herbarium of the British Museum). The establishment of an *A. nodosum* biotope in artificial sheltered habitats on Helgoland followed its spread via seawalls throughout the southern North Sea (Tittley 1986).

The construction on Helgoland of harbour seawalls comprising a vertical wall often protected by an outer armouring of boulders has created an 'extremely wave-exposed' habitat. It supports the prominent and extensive '*Mastocarpus stellatus* biotope' (ID 12) at mid eulittoral levels. This biotope is common in such conditions in the natural rocky shores of Britain but only became established on Helgoland following accidental introduction of a population in the 1980s (Bartsch and Kuhlenkamp 2000). A recently discovered specimen from Helgoland dated 1837 (Kiel) of fertile *M. stellatus* attached to a rock fragment (Kuhlenkamp, personal observation) demonstrates the potential for the natural spread of this species to Helgoland. However, there are no other records indicating the existence of a former natural population. It is unknown how the recent spread of *M. stellatus* has altered the extent of other biotopes or species. Comparison of photographs taken at the same place at the bunker remains in the northeast in 1986 and 2001 shows the change from a '*Mytilus* rock' sensu Janke (1986) with dense *Mytilus edulis* Linnaeus beds and sparse *Fucus* spp. cover to a MLR.BF.Fser.R biotope (ID 16.1) with dense *Fucus* spp. and *M. stellatus* cover and *M. edulis* underneath (Fig. 2).

The '*Sargassum* variant' is also new to Helgoland and became established after 1988 (Bartsch and Kuhlenkamp 2000). It probably has altered the appearance and function of the 'Fucoid and kelp' and the '*Corallina*' biotopes with the invasion of rockpool sites; unfortunately there is no recorded information on the spread of this vigorous species. A recent re-investigation of the fauna of the northeastern wave-cut platform showed that *Halidrys siliquosus* was not present at sites at sublittoral fringe levels where it was recorded in 1986–1990 (Reichert 2003). It formerly grew among *Laminaria digitata* and created habitat for epibenthos. Other *H. siliquosus* habitats such as deep rockpools with sand and gravel and '*Corallina*'-dominated channels are now abundantly colonised by *S. muticum* in summer. Dense stands of *H. siliquosus* at sublittoral fringe levels were still present near the bunker remains in winter 2004 with a few degraded *S. muticum* plants, indicating a mutual existence of both species but with a seasonal shift of abundance. Both observations suggest competition for space between *S. muticum* and *H. siliquosa*. Where *H. siliquosa* was the dominant species in the pool biotope characterised as FLR.Rkp.FK (ID 7), it would be better considered as a second variant (FLR.Rkp.FK.Hal) to distinguish between the native and invasive aspects.

The former nature of cliff and cave habitats is illustrated in Kuckuck (1897b, Fig. 2 and plate 8). These were mostly lost after seawall construction in the early twentieth century. The cave biotope at eulittoral fringe levels characterised by a thin felt of the brown algae *Pilinia rimosa* Kützing and *Pleurocladia lucifuga* (Kuckuck) Wilce (= *Ectocarpus lucifugus* Kuckuck; Kuckuck 1897b) is presumed to be extinct despite growth of *P. rimosa* under *Fucus* spp. at the base of Breithorn cliff (Tittley 1982; see Table 3 'cave community'). There is now only a single cave with algal growth at supralittoral fringe levels in the north of the island; it is subject to considerable erosion and may collapse.

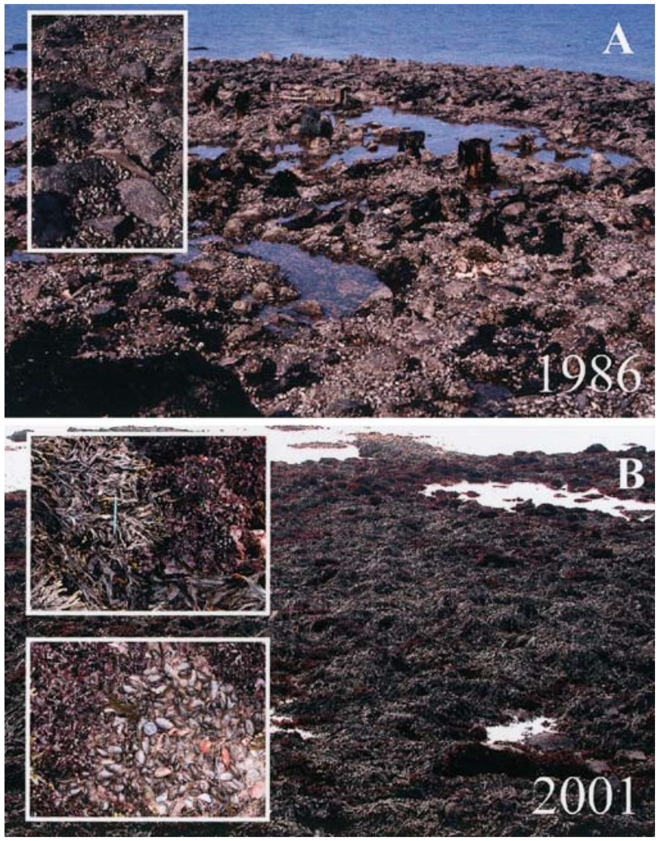


Fig. 2A, B Biotope change in the mid eulittoral zone at Helgoland, bunker remains in the northeast, between 1986 and 2001 after the introduction of the red alga *Mastocarpus stellatus*. The same site is shown in (**A**) 1986 (*Mytilus edulis* beds with sparse *Fucus* spp. cover) and in (**B**) 2001 (dense *Fucus* spp./*Mastocarpus stellatus* cover over *Mytilus edulis*)

Previous descriptions of shore ecology and floristic accounts suggest three other biotopes to have been formerly present on the island. The '*Calothrix*/*Bangia*' association and a '*Ralfsia* assemblage' formed zones at supralittoral levels on concrete blocks and a small epiphyte-free sublittoral *Zostera marina* bed was present at a site in the east of the island at 5-m depth that was later lost because of land reclamation. It has proved difficult to relate the first two assemblages to the biotopes described by Connor et al. (1997a, 2003). Although *Bangia atropurpurea* (Roth) C. Agardh patches were present in late winter and *B. atropurpurea* was a common constituent of the '*Ulothrix*/*Urospora* biotope', the distinct belt of *B. atropurpurea* on seawalls and harbour walls described by Nienburg (1930), Munda and Markham (1982), and Brünger (1989) was not found in this study. An algal community characterised by *B. atropurpurea* was not considered to be a distinct biotope by Connor et al. (1997a, 2003). Although *Ralfsia verrucosa* (Areschoug) Areschoug was commonly present as a crustose layer within the HLR.MusB.Sem.LitX biotope (ID 11.2) and the two '*Mytilis*' biotopes (MLR.MusF.MytFR and MLR.MusF.MytFves; IDs 13 and 14), a distinct belt at littoral fringe level was missed in this study.

The biotopes characterised by *Mytilus edulis* or *Littorina* spp. (MLR.MusF.MytFves, MLR.MusF.MytFR and HLR.MusB.Sem.LitX) probably only developed to their present extent after the early 1950s, although the botanical focus of earlier studies might have overlooked their former existence. During the 1980s the *Mytilus* beds on the northeastern wave-cut platform were described as part of the *Fucus* vegetation (Janke 1986; Reichert 2003) and were not considered to be a separate assemblage despite an unpublished photograph taken by Janke in 1986 showing extensive *Mytilus* beds in the same location as those recorded in this study. More recently Janke (1990) considered them to be distinct. The '*Littorina*/barnacle'-characterised biotope in the southwest corner of Helgoland ('Kringel'; HLR.MusB.Sem.-LitX; ID 11.2) probably developed as a consequence of geological and habitat change following an explosion that destroyed part of Helgoland in 1947 (Herms 2002). The fracturing of the upper red sandstone and the formation of a mobile layer of cobbles and boulders on the wave-cut platform created a different type of habitat.

Although the natural coastal environment of Helgoland and Dune is dynamic and has changed considerably during recent historical times, the effect on marine biotopes is largely unknown. Apart from the changes described above, appraisal of past descriptive ecological accounts suggests that most biotopes at mid eulittoral levels and below have remained present and probably stable over the past 100 years; changes in spatial extents of these biotopes are largely unknown except for the changes that have taken place at the bunker remains in the northeast (Figs. 1, 2). As the perennial flora is the characterising feature of most biotopes, stability can be inferred from the floristic accounts of Kornmann and Sahling (1994) and Bartsch and Kuhlenkamp (2000).

Conclusion

This study on the biotopes of Helgoland complements recent floristic and faunistic studies; together they create a comprehensive baseline of information that can be used in future studies on change in biodiversity at species and community levels. The British biotope classification and method works well on Helgoland and required only minor changes to reflect local biodiversity and ecology. Our ultimate goal of mapping the spatial extents of benthic intertidal biotopes will supply another quantitative value for the intertidal biota and thus allow more objective monitoring of change. Such data will support decision making in the management of the intertidal ecosystem of Helgoland, which is an important nature conservation area. In view of concerns about the impact of introductions, and also about global warming and concomitant increase in sea temperatures and rise in sea level, the creation of a baseline of biotope data using an accepted and workable system of community classification is timely. As four of the biotopes and variants of Helgoland were considered rare or scarce by Connor et al. (1997a) for Britain and Ireland, their occurrence on Helgoland is of regional and international conservation importance. The present study has contributed to the recognition of biotopes in a more extensive biogeographical region than Britain and Ireland, and their local stability with time.

Acknowledgements The co-author (IT) gratefully acknowledges financial support from the Alfred Wegener Institute to undertake fieldwork on Helgoland. The authors are grateful to K. Janke for the permission to publish his photograph taken in 1986. K. Doelle is thanked for her accurate and tedious work in digitising the map of the intertidal zone of Helgoland. J. Weber is thanked for his support concerning the creation of the orthophotographs of Helgoland.

References

Bartsch I, Kuhlenkamp R (2000) The marine macroalgae of Helgoland (North Sea): an annotated list of records between 1845 and 1999. Helgol Mar Res 54:160–189

Brünger S (1989) Vegetationskundliche Untersuchungen über die Flora des Helgoländer Felswatts im Eulitoral und oberen Sublitoral. Diploma work, University of Karlsruhe

Caspers H (1938) Die Bodenfauna der Helgoländer Tiefen Rinne. Helgol Wiss Meeresunters 2:1–112

Choi H-G, Kim M-S, Guiry MD, Saunders GW (2001) Phylogenetic relationships of *Polysiphonia* (Rhodomelaceae, Rhodophyta) and its relatives based on anatomical and nuclear small-subunit rDNA sequence data. Can J Bot 79:1465–1476

Connor D, Brazier DP, Hill TO, Northen KO (1997a) Marine nature conservation review: marine biotope classification for Britain and Ireland, vol 1. Eulittoral biotopes. Version 97.06. (JNCC rep no 229) Joint Nature Conservation Committee, Peterborough

Connor D, Dalkin MJ, Hill TO, Holt RHF, Sanderson WD (1997b) Marine nature conservation review: marine biotope classification for Britain and Ireland, vol 2. Sublittoral biotopes. Version 97.06. (JNCC rep no 230) Joint Nature Conservation Committee, Peterborough

Connor DW, Allen JH, Golding N, Lieberknecht LM, Northen KO, Reker JB (2003) The national marine habitat classification for Britain and Ireland. Version 03.02. Joint Nature Conservation Committee, Peterborough, Littoral Rock Section. http://www.jncc.gov.uk/MarineHabitatClassification Cited Dec 2003

Dalla-Torre KW von (1889) Die Fauna von Helgoland. Zool Jahrb Syst Ökol Geogr Tiere 4 (Suppl):1–99

Den Hartog C (1959) The epilithic marine algal communities of the Netherlands coast. Wentia 1:1–241

Dierschke H (1994) Pflanzensoziologie. Eugen Ulmer, Stuttgart

Foster-Smith R (2001) Biotope mapping in the coastal zone. A manual for mapping shore biotopes of West Africa. Version 2, May 2001. West African Darwin Initiative Project, Newcastle-upon-Tyne

Gillandt L (1979) Zur Ökologie der Polychaeten des Helgoländer Felslitorals. Helgol Wiss Meeresunters 32:1–35

Götting K-J (2001) New records of prosobranch and heterotroph gastropods (Mollusca, Gastropoda) in the German Bight. Jh Ges Naturkd Württemberg 157:211–239

Herms M (2002) Flaggenwechsel auf Helgoland. Links, Berlin
Hiscock K (1996) Marine nature conservation review: rationale and methods. Joint Nature Conservation Committee, Peterborough
Janke K (1986) Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. Helgol Wiss Meeresunters 40:1–55
Janke K (1990) Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgol Meeresunters 44:219–263
John DM, Foster-Smith R, Paterson GL, Ramírez ME, Evans NJ, Spencer Jones ME, Reid DG, Ferrero TJ (2002) A 'biotope' approach to the marine benthic biological assemblages of the Laguna San Rafael National Park, Chile. Bol Mus Hist Nat Chile 51:159–173
Kent M, Coker P (1992) Vegetation description and analysis. A practical approach. Bellhaven Press, London
Kluijver MJ de (1991) Sublittoral hard substrate communities off Helgoland. Helgol Meeresunters 45:317–344
Kornmann P, Sahling P-H (1977) Meeresalgen von Helgoland. Helgol Wiss Meeresunters 28:217–225
Kornmann P, Sahling P-H (1983) Meeresalgen von Helgoland, Ergänzung. Helgol Meeresunters 36:1–65
Kornmann P, Sahling P-H (1994) Meeresalgen von Helgoland. Zweite Ergänzung. Helgol Meeresunters 48:365–406
Kuckuck P (1894) Bemerkungen zur marinen Algenvegetation von Helgoland. Wiss Meeresunters (Abt Helgol) 1:225–263
Kuckuck P (1897a) Über marine Vegetationsbilder. Ber Dtsch Bot Ges 15:441–447
Kuckuck P (1897b) Über zwei höhlenbewohnende Phaeosporeen. Wiss Meeresunters (Abt Helgol) 2:35–370
Kuckuck P (1897c) Bemerkungen zur marinen Algenvegetation von Helgoland II. Wiss Meeresunters (Abt Helgol) 2:373–400
Lange H (1970) Die Algenzonierungen im Litoral und Sublitoral um Helgoland. Nat Mus 100:153–167
Lüning K (1970) Tauchuntersuchungen zur Vertikalverteilung der sublitoralen Helgoländer Algenvegetation. Helgol Wiss Meeresunters 21:271–291
Lüning K (1990) Seaweeds. Their environment, biogeography, and ecophysiology. Wiley, New York
Munda IM, Kremer BP (1997) Morphological variation and population structure of *Fucus* spp. (Phaeophyta) from Helgoland. Nova Hedwigia 64:67–86
Munda IM, Markham JM (1982) Seasonal variations of vegetation patterns and biomass constituents in the rocky eulittoral of Helgoland. Helgol Meeresunters 35:131–151
Nienburg W (1930) Die Besiedlung des Felsstrandes und der Klippen von Helgoland II. Die Algen. Wiss Meeresunters (Abt Helgol) 15:1–15
Reichert K (2003) Die Makrofauna und ihre räumliche Verteilung und saisonale Veränderung im Felswatt von Helgoland. Ein Vergleich zur Untersuchung von 1984. Diploma thesis, University of Hamburg
Rueness J, Brattegard T, Lein TE, Küfner R, Pedersen A, Sorlie AC (1997) In: Brattegard T, Holthe T (eds) Distribution of marine benthic macro-organisms in Norway: a tabulated catalogue, preliminary edn. (Research report for DN no 1997-1) Directorate for Nature Management, Trondheim, pp 22–64, 337–350
Schmidt OC (1928) Die Algenvegetation Helgolands. In: Karsten G (ed) Vegetationsbilder 19. Reihe, Heft 5, plates 25–30. Fischer, Jena
South GR, Tittley I (1986) A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History), St. Andrews
Tittley I (1982) The effects of man made constructions on the marine flora of the southern North Sea. MPhil thesis, The Open University
Tittley I (1986) Seaweed communities of the artificial coastline of southeastern England 2. Open sea-shore. Trans Kent Field Club 10:55–67
Tittley I, Neto AI (2000) A provisional classification of algal-characterised rocky shore biotopes in the Azores. Hydrobiologia 440:19–25
Tittley I, Gilliland P, Pound D (1998) Marine flora of the Thanet Coast cSAC: a conservation and management perspective. In: Scott GW, Tittley I (eds) Changes in the marine flora of the North Sea. Centre for Research into Coastal Issues, Scarborough, pp 65–75
Ziegelmeier E (1957) Die Muscheln (Bivalvia) der deutschen Meeresgebiete. Helgol Wiss Meeresunters 6:1–64
Ziegelmeier E (1966) Die Schnecken (Gastropoda, Prosobranchia) der deutschen Meeresgebiete und der brackigen Küstengewässer. Helgol Wiss Meeresunters 13:1–61