J. Mar. Biol. Ass. U.K. (2004), **84**, 1169–1177
Printed in the United Kingdom

Habitat and distribution of the warm-water barnacle *Solidobalanus fallax* (Crustacea: Cirripedia)

A.J. Southward*[§], K. Hiscock*, F. Kerckhof[†], J. Moyse[‡] and A.S. Elfimov[∫]

*Marine Biological Association, Citadel Hill, Plymouth, PL1 2PB, UK. [†]MUMM, Marine Environmental Management Section, Royal Belgian Institute of Natural Sciences, 3e en 23e Linieregimentsplein, B-8400, Oostende, Belgium. [‡]336 Gower Road, Swansea, SA2 7AE, Wales, UK. [∫]Department of Invertebrate Biology, Moscow State University, Moscow 119899, Russia. [§]Corresponding author, e-mail: ajs@mba.ac.uk

New records are given of the occurrence of the warm-water barnacle *Solidobalanus fallax* in Britain and Europe. This barnacle is not found on rocks or stones, but settles on biological substrata, including algae, cnidarians, bivalves, gastropods and crustaceans. It also settles on plastic bags and nets, plastic-coated objects such as crab and lobster pots and octopus pots made of ceramic or plastic. With one exception the species was unrecorded in Europe before 1980; it may have increased in abundance during recent years as a result of rising temperatures. The cyprid larvae, which can metamorphose on plastic Petri dishes, appear to be adapted to seek out 'low energy' surfaces. One of the habitats colonized by *S. fallax* is the sea-fan *Eunicella verrucosa*, where it seems to have increased in recent years, possibly to the detriment of the cnidarian host. *Solidobalanus fallax* has the potential to be a serious pest of fish-farming structures to the south of Britain.

INTRODUCTION

In recording *Solidobalanus fallax* (Broch) in the western English Channel off Plymouth in 1994 (Southward, 1995) it was stated that this species was found exclusively on the queen scallop, *Aequipecten opercularis* (L.), predominantly on the upper valve. There have been subsequent records of this barnacle on other biological substrata and on plastics. As previously noted (Southward, 1995), *Solidobalanus fallax* may have been missed by collectors who confused it with *Balanus crenatus* Bruguière. The more whitish specimens of *S. fallax* can be mistaken for *B. crenatus*, but when their shells show reddish-purple patches they are conspicuous, and when they occur in great numbers are easy to distinguish. *Solidobalanus fallax* tends to be smaller but relatively taller than *B. crenatus*; if the outside of the shell is cleaned they can be seen to have colouring of some or all the parietes. The scutum is also coloured and shows strong growth ridges. If placed in seawater and allowed to open the valves, *S. fallax* shows tergo-scutal flaps with brown or black banding on a yellow field. Shells of *S. fallax* can be distinguished from *B. crenatus* by the solid walls, without the pores (longitudinal canals) found in the latter.

Records since 1995 are given here and also earlier findings rediscovered recently. The choice of substratum by this barnacle is discussed in the light of possible selection of surfaces by the cypris larva.

MATERIALS AND METHODS

Specimens were recovered by dredging, trawling, SCUBA diving and examination of floating structures, lobster/crab pots, octopus pots and stranded objects. Once this barnacle was known to occur on substrata other than queen scallop shells, active searches were made, particular attention being paid to colonies of the sea-fan, *Eunicella verrucosa* (Pallas). SCUBA-diving colleagues who were asked to examine their log-books and photographs of the sea-fan provided much supplementary information. Further evidence of the presence of *Solidobalanus fallax* has been gathered during field excursions by one of us (F.K.) along the south Iberian peninsula, the west Atlantic coast of Portugal and Spain, and the north and west coasts of France. The species was searched for in harbours, on lobster pots and other fishing gear and colleagues were briefed how to recognize it during their visits to these coasts.

NEW RECORDS FROM THE BRITISH ISLES

Devon and Cornwall

Table 1 lists post-1994 records of *Solidobalanus fallax* from the Plymouth inshore fishing grounds. Table 2 lists records by SCUBA diving off South Devon and East Cornwall as far west as the Lizard peninsula and at Lundy Island in the Bristol Channel. The first inkling that this barnacle was eclectic in its choice of habitat was provided by samples of the sea-fan *Eunicella verrucosa* collected by Roger Swinfen on the cliffs of the Mewstone, off Plymouth Sound, in 1995. The sea-fans were being used by shags, *Phalacrocorax (Stictocarbo) aristotelis* (L.), as nesting material. Several specimens of *Solidobalanus fallax* were attached to the sea fans.

Figure 1 shows *Solidobalanus fallax* growing on plastic substrata. Figure 1A,B illustrate settlement on a plastic shopping bag, trawled up in Whitsand Bay, south-east Cornwall, the bag apparently originating from a fish shop in Taunton, Somerset; Figure 1C,D show settlement on a

Table 1. *Records of* Solidobalanus fallax *recovered on the Plymouth inshore grounds since 1994.*

Date	Location	Number of *Solidobalanus*	Notes
02-Jun-95	4 nm south of the Mewstone	5	one tub of queen scallops, from fish market
05-Jun-95	Eddystone grounds	6	two tubs of queen scallops, from fish market
13-Jun-95	10 hauls with Agassiz between Rutts	2	on dead queen scallop shell
		1	on *Buccinum* shell inhabited by *Eupagurus*
29-Jun-95	trawl off West Rutts, 45 m	17	on queen scallops
		14	on *Buccinum* shells inhabited by *Eupagurus*
		15	on rubber-covered frame of crab pot and plastic rope
29-Jun-95	trawl Bigbury Bay, 39 m	2	on *Maia squinado*
26-Jul-95	trawl Bigbury Bay, 33 m	4	2 each on two *Maia squinado*
		4	on *Buccinum* shells inhabited by *Eupagurus*
26-Jul-95	trawl Bigbury Bay, 30 m	5	on 5 *Maia squinado*
26-Jul-95	trawl Bigbury Bay, 30 m	9	on 1 *Maia squinado*
14-Aug-95	trawl Bigbury Bay	3	on queen scallops
31-Aug-95	trawl off Looe Island, 40 m	5	on queen scallops
Oct-95	nest of shag, Mewstone	several	on *Eunicella* used to line nest
08-Nov-95	dredge off Hillsea ('Stoke') Point	clusters up to 10 each	on 4 out of 24 colonies of *Eunicella*
	dredge off Hillsea ('Stoke') Point	1	on *Scalpellum* growing on *Eunicella*

Table 2. *Records of* Solidobalanus fallax *made by SCUBA diving since 2000.*

Date	Location	Notes
11-Oct-00	the submerged cliff line off Plymouth Sound, 39 m*	on *Eunicella*; much epibionts as well as barnacles
14-Jul-02	the submerged cliff line off Plymouth Sound, 25 m	on *Eunicella*; several clusters
30-Jul-02	Petes Pinnacle, Lundy Island, 28 m	on *Eunicella*; produced nauplii on transfer to aquarium
02-Aug-02	wreck of 'Rosehill', west Whitsand Bay, 29 m	on *Eunicella*; one colony with many barnacles (Figure 2D)
07-Dec-02	the submerged cliff line off Plymouth Sound, 36 m	on *Eunicella*, up to 10% colonies with epibionts
15-Feb-03	Hand Deeps, 33 m	on *Eunicella*, only 0.5 to 1% of sea-fans had tissue loss
16-Feb-03	wreck of 'Rosehill', west Whitsand Bay, 29 m	on *Eunicella*
22-Mar-03	the submerged cliff line off Plymouth Sound, 34 m	on *Eunicella*; up to 10% of sea-fans have epibionts
25-Jul-03	the Manacles, Raglan reef, 30 m	on *Eunicella*, only one colony with barnacles
12-Oct-03	the submerged cliff line off Plymouth Sound, 42 m	'meadow' of *Eunicella*, about 3% infested with barnacles
15-Nov-03	Hatt Rock (west of the Eddystone), 23 m	about 10% of *Eunicella* carrying barnacles
15-Nov-03	Hatt Rock (west of the Eddystone), 23 m	one small cluster on the hydroid *Gymnangium montagui* (Billard)
06-Dec-03	the submerged cliff line off Plymouth Sound, 30 m	on *Eunicella*, up to 50% carrying barnacles
10-Jan-04	the submerged cliff line off Plymouth Sound, 30 m	on platform about 10% *Eunicella* carry barnacles but on cliff edge and in gullies up to 50% infested

*, The submerged cliff line off Plymouth Sound is a popular location for SCUBA diving. It was described by Cooper (1948) as lying 2 nautical miles south-south-west of the Breakwater Lighthouse, a gradient of 1 in 3 from 27 to 44 metres below chart datum.

nylon monofilament fishing net washed up in North Wales; specimens on plastic from Portugal are shown for comparison in Figure 1E,F. Figure 2 shows its occurrence on sea-fans. Figure 2A is a normal 'meadow' of sea-fans, with low incidence of the barnacle, while Figure 2B,D show heavy infestation of the sea-fans. Figure 2C shows a less dense infestation on *Eunicella*, and Figure 2E is a closer view of the same cluster of *S. fallax* in life. Figure 3A,B show *S. fallax* on the carapace of *Maia squinado* (Herbst); Figure 3C shows specimens near the tip of the spire of a shell of *Buccinum undatum* L. inhabited by *Eupagurus bernhardus* (L.).

There is a sole record for the far west of Cornwall. A dredge catch taken off the Runnelstone, south-west Cornwall, in 1988 included some hydroids to which barnacles were attached. Re-examination of these barnacles shows them to be *Solidobalanus fallax*. Station A1, 'Challenger' cruise 32/1988, 63 m deep, 50°00.6′N 5°38.3′W, therefore constitutes the earliest record of the species in the English Channel.

It is evident that the species is widespread on biological and synthetic substrata off Devon and Cornwall. Occurrence on *Eunicella* ranges from 0.5 to 50%, with particularly heavy settlement on colonies that have lost part of the living tissues through other causes (Table 2, Figure 1).

Dorset

Solidobalanus fallax has been noted on colonies of the sea-fan washed ashore at Chesil Beach between West Bexington and Abbotsbury (P. Tinsley, personal communication). It was also reported in 1998 on a lobster pot on the

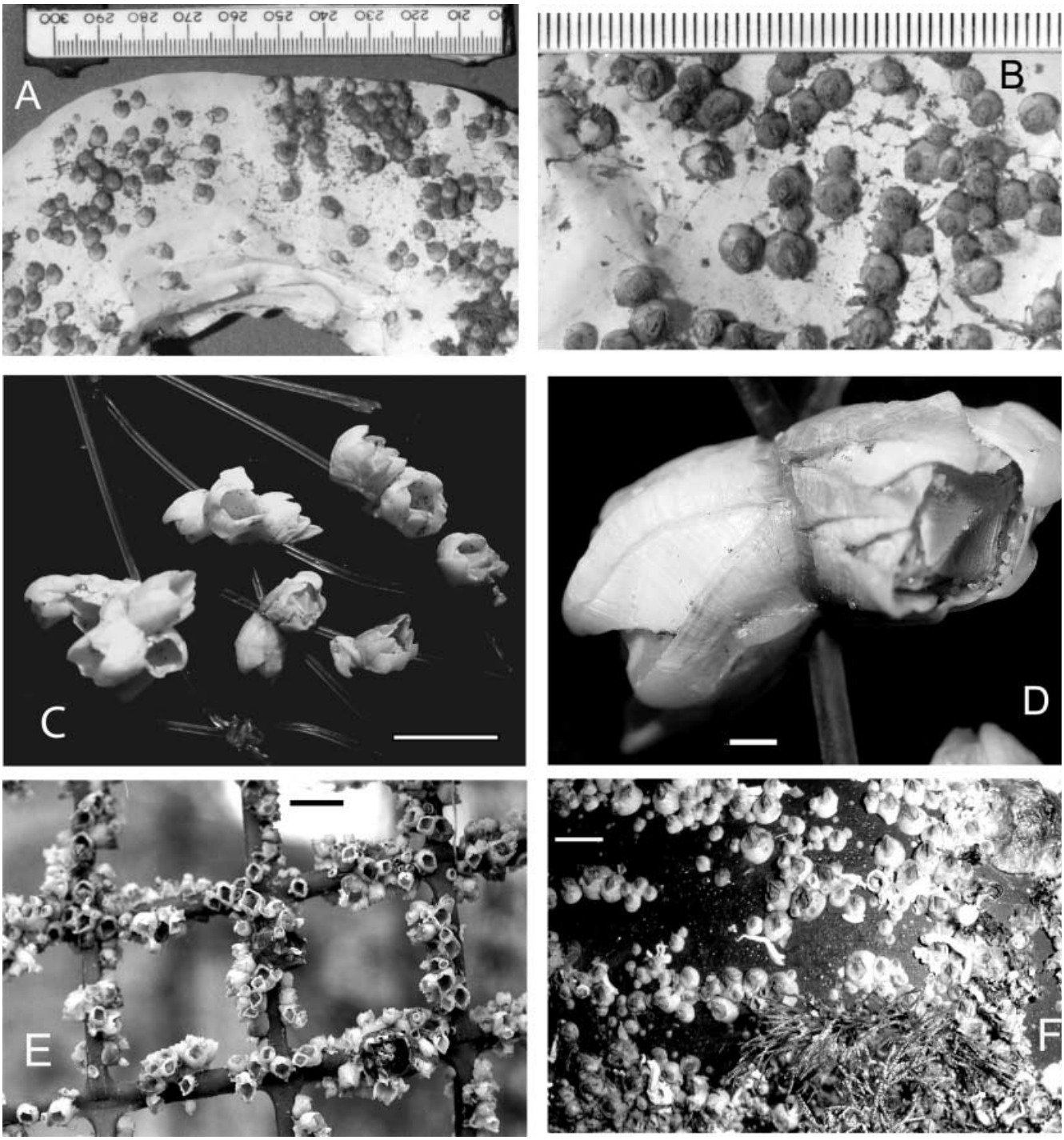

Figure 1. *Solidobalanus fallax* growing on man-made materials: (A) the handle region of a plastic bag trawled in Whitsand Bay, 4 April 1996, with many *S. fallax*; (B) closer view of the *S. fallax* on the plastic bag; (C) *S. fallax* growing on nylon monofilament netting, washed up on Anglesey in 2003; (D) a closer view of C showing how the barnacle bases meet and surround the narrow nylon filament; sand grains from the beach where the netting washed up are visible; (E) many *S. fallax* and a few *Megabalanus tulipiformis* on the netting of a lobster pot at Portimao, Algarve, Portugal, November 2003; (F) plastic octopus pot at Tavira, Algarve, November 2003, showing many *S. fallax*, with growths of *Pomatoceros triqueter*, *Bugula neritina* and *Anomia ephippium* (photograph courtesy F. Cardigos, Departmento de Oceanografia e Pesca, University of the Azores). Scale bars: A&B, millimetre rules; C, E&F, 10 mm; D, 1 mm.

quayside in Portland Harbour (J. Haelters, personal communication).

Lundy Island, Bristol Channel

The occurrence of *Solidobalanus fallax* on *Eunicella* at Lundy is noted in Table 2.

Wales

In February 1995 *Solidobalanus fallax* was quite plentiful on the holdfasts of *Laminaria hyperborea* (Gunn.) Foslie at Oxwich Bay, south Gower Peninsula in South Wales (Figure 3D). Alan Osborn, then Chief Technician of the Department of Zoology, University of Wales, Swansea,

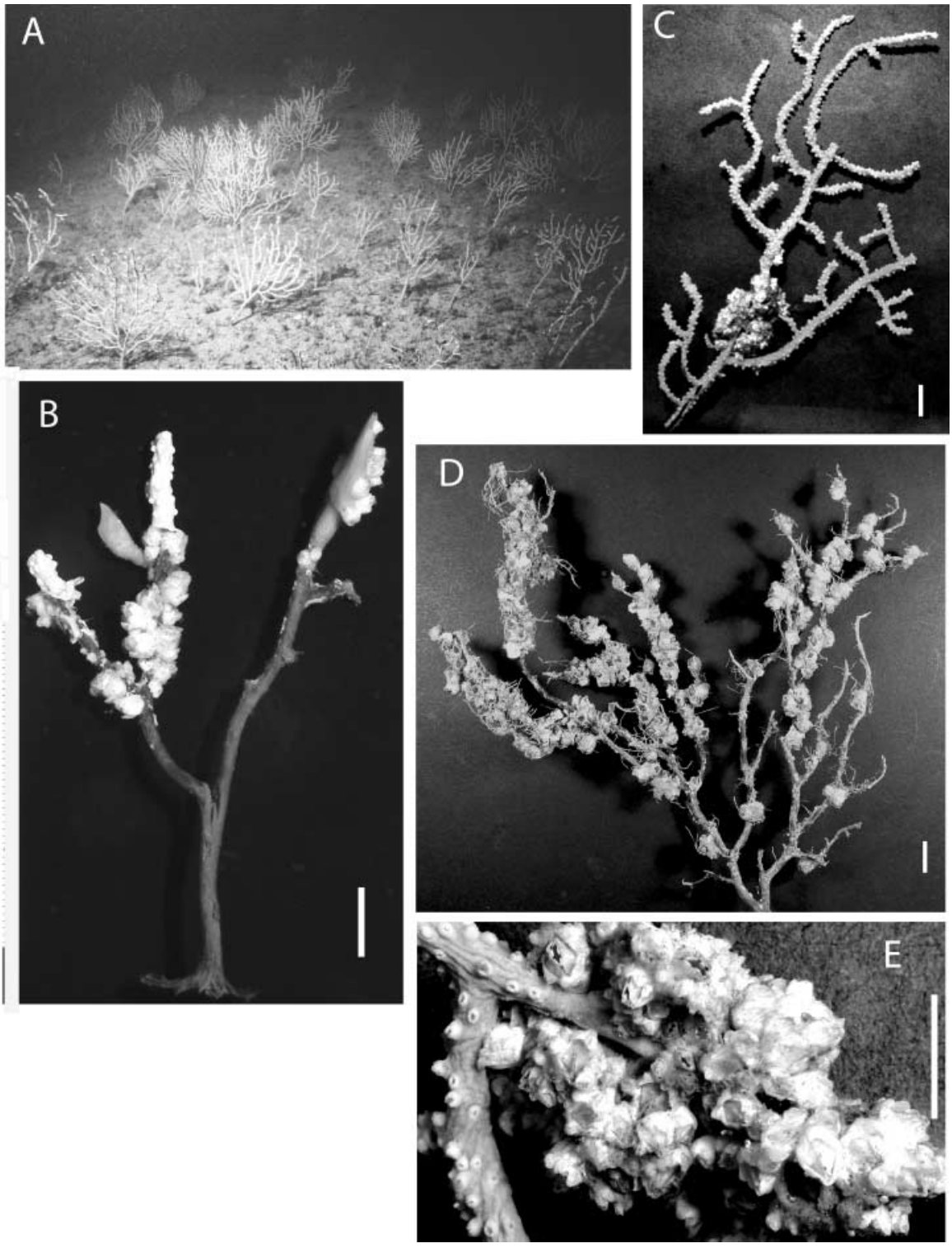

Figure 2. Settlement of *Solidobalanus fallax* on the sea-fan *Eunicella verrucosa*: (A) typical 'meadow' of the sea-fan with little infestation by *S. fallax* or other epibionts; (B) a sea-fan from Hilsea ('Stoke') Point, November, 1995, photographed after preservation, showing medium infestation by *S. fallax* and also the stalked barnacle *Scalpellum scalpellum*; (C) light infestation by *S. fallax* on a sea-fan from the submerged cliff line off Plymouth Sound (see Table 2); (D) sea-fan heavily infested by *S. fallax*, wreck of 'Rosehill', Whitsand Bay, photographed dry; (E) a close view of the cluster shown in C, live barnacles displaying characteristic brown to black banding of the tergo-scutal flaps. Note that the sea fans shown in B and D have lost a substantial part of the coenenchyme. Scale bars: 10 mm.

who collected the sample, thinks similar barnacles had been present on *Laminaria* on the Gower coast for ten years or more. It is believed that the *S. fallax* could have been mistaken for another warm-water barnacle, *Balanus amphitrite* (Darwin), which used to occur earlier in the Queen's Dock at Swansea and which survived for a while after cessation of the power station warm effluent (Bullimore et al., 1978), but which ultimately was replaced

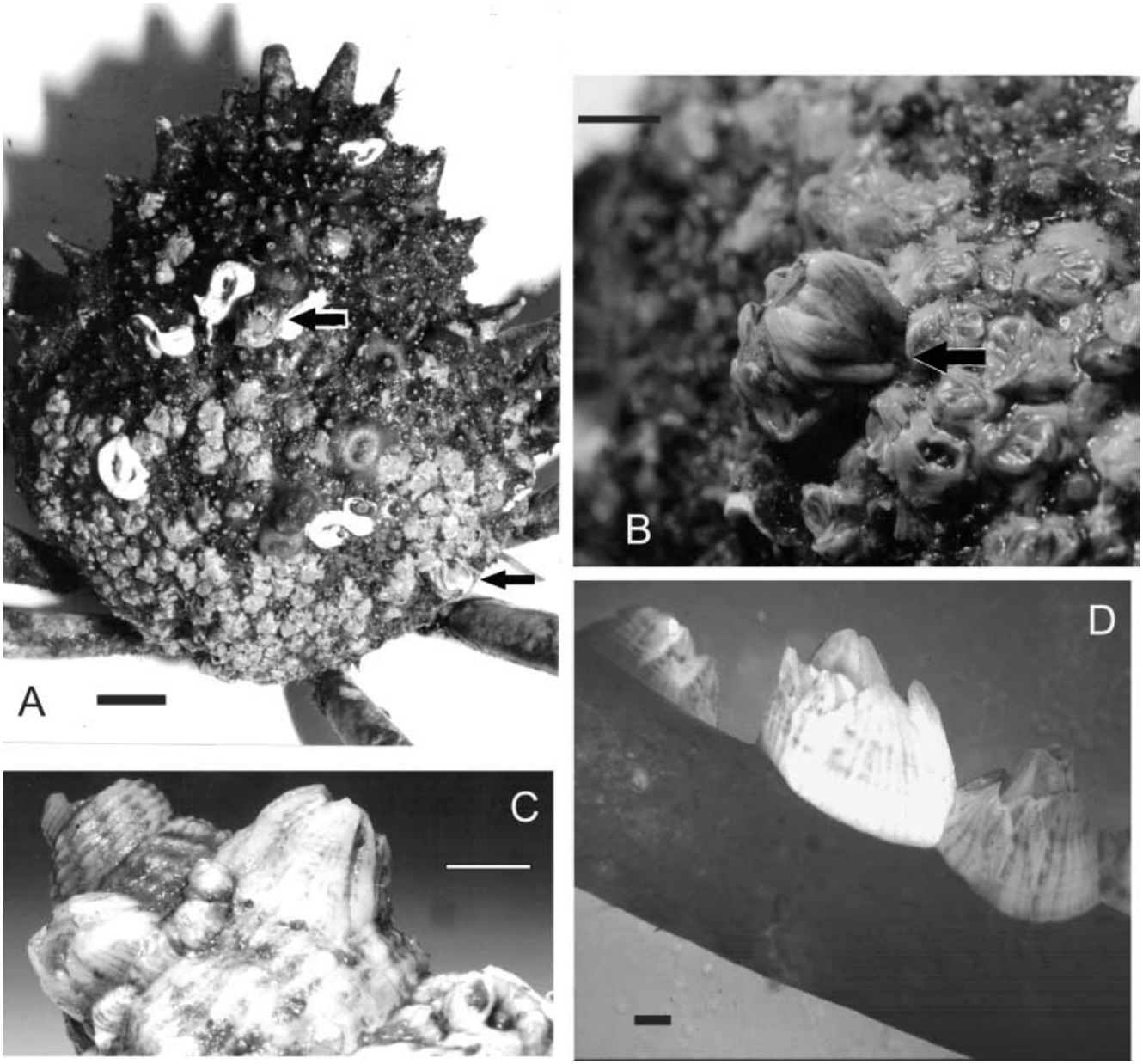

Figure 3. (A) *Solidobalanus fallax* on the carapace of the spider crab, *Maia squinado* (arrows), the other epibionts are serpulid polychaetes and the barnacle *Verruca stroemia* (O.F. Müller); (B) closer view of *S. fallax* on *Maia*, surrounded by *Verruca*; (C) two *S. fallax* on the shell of a *Buccinum* inhabited by *Eupagurus*; (D) *S. fallax* on the holdfast of *Laminaria*, Oxwich Bay, South Wales. Scale bars: A, 10 mm; B,C, 5 mm; D, 1 mm.

by *Balanus crenatus* (P. Dyrynda, personal communication). Observers diving off Skomer Island, surveying *Eunicella verrucosa* since 1964, have not seen *S. fallax* (Mark Burton, personal communication).

During 2000 and 2001 members of the Belgian Strandwerkgroep (including F.K.) visited South Wales and in particular the Pembrokeshire coast. Searches were made along the strandline or in harbours and *Solidobalanus fallax* was found present but not abundant in August 2000 on lobster pots in Fishguard harbour and in April 2001 it was present on stranded objects on the beach at Freshwater West.

The most recent find of the species is from North Wales, attached abundantly to a monofilament nylon fishing net washed ashore on the beach north of Llanddwyn Island, south-west Anglesey, 21 July, 2003 (E.I. Rees, personal communication). This net was judged to have been lying on the seabed for some time before being washed ashore, and then had been long enough on the beach for the barnacles to dry out. A few specimens still retained the opercular plates (Figure 1D) and dried cirri, allowing certainty over the identification. The barnacles were all about the same size, about 5 mm rostro-carinal diameter and up to 6 mm high, equivalent in size to the settlement found on the plastic bag off Plymouth in 1996. Most probably they had settled the previous autumn, the species being a summer and autumn breeder (Southward, 1995; Korn & Elfimov, 1999; Korn et al., 2001). Knowledge of hydrographic factors and fishing techniques suggests that the settlement took place to the south of Anglesey, in the Celtic Sea or outer Bristol Channel.

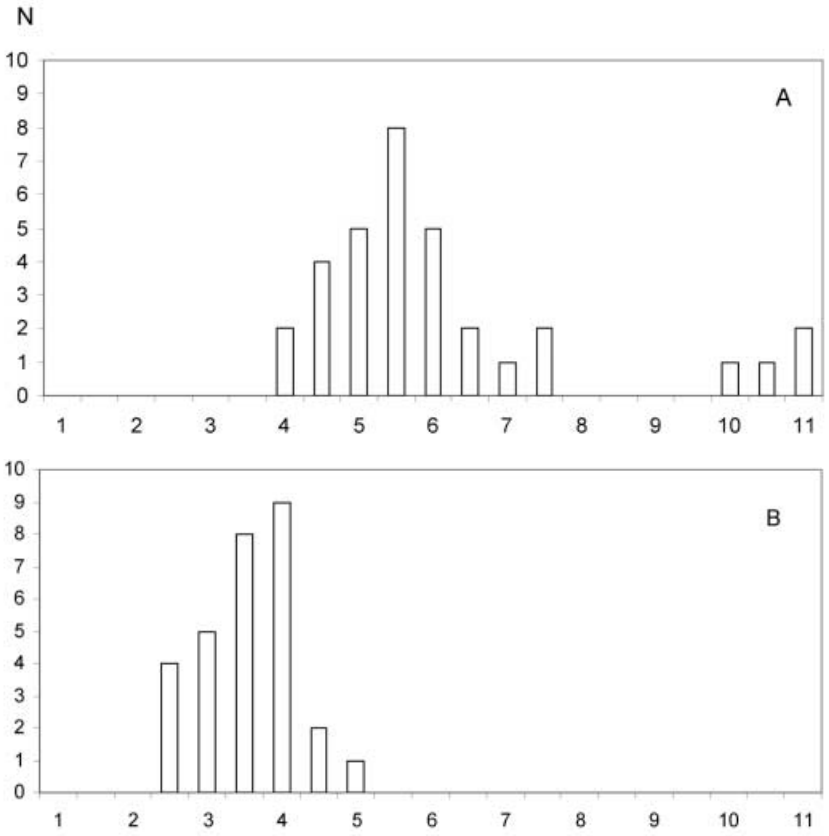

Figure 4. Size-frequency distributions (0.5 mm classes) of samples of *Solidobalanus fallax*: (A) on shells of queen scallops trawled between the Rutts, 40 m, 10 & 20 May, 1994; (B) on the plastic bag trawled in Whitsand Bay, 4 April 1996.

Channel Islands

We have no direct records but in August 2001 a set of lobster pots was seen by F.K. at a warehouse in the fish market of Oostende. Amongst the fouling organisms on these pots were many *Solidobalanus fallax*. The owner reported that he bought the pots in January 2001 in Guernsey; they had not been deployed since.

NEW AND EXISTING RECORDS FOR OTHER PARTS OF EUROPE

Solidobalanus fallax was reported from the Meteor Seamount, south of the Azores, collected by FS 'Meteor' 1966–1975 (Young, 1998). It co-occurred with *Megabalanus tulipiformis* (Ellis) and *Balanus spongicola* Brown but no details were given of depth or substratum. There is an earlier record of the species in Portuguese waters, recently identified by R.-P. Carriol (personal communication) as occurring in a sample collected in 1957 in 43 m depth, Station 'Faial' SME 1188, 38°16′N 8°49.2′W (detected H. Zibrowius).

The gap in the distribution of *Solidobalanus fallax*, between Morocco and the English Channel, reported earlier (Southward, 1995), is being filled with new records along west European coasts, from southern Spain and Portugal round to the southern bight of the North Sea. We give these separately for the Iberian coast and for the Channel coast of France and the Low Countries. In addition to our own records we include data published recently by Castric-Fey (1996), Castric-Fey et al. (2001), and Carriol (2001).

Iberian Peninsula

Apparently now a common species, *S. fallax* has not previously been recorded from Portugal.

Southern Iberian Peninsula

Evidence gathered during field trips from 2000 to 2003 along the Portuguese south coast (Algarve) and the adjacent south-western Spanish coast showed the species to be common in every fishing harbour along the whole coast from Isla Cristina, (Huelva, Costa de la Luz, Spain), to Sagres (Algarve, Portugal), including Lagos, Portimão, Albufeira, Quartera, the Ria de Faro and Olhaõ Tavira. The typical substrata were lobster pots (with plastic netting; Figure 1E), octopus pots (both plastic and ceramic; Figure 1F) and various plastic objects such as nets, ropes, litter and small styrofoam buoys. The *Solidobalanus fallax* populations were frequently accompanied by smaller numbers of *Megabalanus tulipiformis* and *Balanus perforatus* and occasionally by *Elminius modestus* Darwin.

Solidobalanus fallax was also present on the sea-fan *Eunicella verrucosa*, and on living molluscs such as *Anomia ephippium* L., *Pteria hirundo* (L.) and *Mytilus galloprovincialis* (L.), but on the latter it was less common than *Balanus perforatus*. It was also present on empty lamellibranch shells, such as *Pinna* sp., *Mactra glauca* (Born), *Acanthocardium* sp. and *Solecurtus* sp., that had apparently been discarded by fishermen. Along the strandline *Solidobalanus fallax* was frequently found not only on plastic litter and discarded netting, but also on small twigs.

Atlantic coast of Portugal and Spain

Solidobalanus fallax was found at Cascais in May 1998 on lobster pots. It was also found between Nazare and Aveiro in July 1999 on stranded plastic objects and debris including octopus pots and on a styrofoam buoy. At both places it was accompanied by *Megabalanus tulipiformis* and *Balanus perforatus*.

Investigations in June 2004 showed *Solidobalanus fallax* to be common on crab pots at La Guardia, near the Portuguese frontier and less common at Bueu (Ria de Pontevedra). It was present on a cable at the yacht harbour of Vigo and also on stranded plastic octopus pots at Lanzada (between the Ria de Pontevedra and the Ria de Arosa).

France

Atlantic coast of France

Solidobalanus fallax appears well established along this coast. We have records from Saint Jean de Luz in August 2001, and from Piriac-sur-Mer and Noirmoutier (Loire Atlantique) in April 1997 (Kerckhof, 1997a).

In Brittany, *S. fallax* is reported present in small numbers in the Morbihan region, the Ria d'Etel, the Glenan region and the Ouessant region by Castric-Fey et al. (2001). Carriol (2001) records several specimens on the Ile de Houat (Morbihan) in August 1999. *Solidobalanus fallax* was found at Le Conquet (Finistère) in April 1998 and August 2003, on lobster pots and on the sea-fan *Eunicella verrucosa*. However, Castric-Fey et al. (2001) report it absent from the Rade de Brest.

English Channel coast of France

In August 2003 *Solidobalanus fallax* was found on *Aequipecten opercularis* brought in by a fisherman at Roscoff. They were not very common.

Along the Corniche-Bretonne/Côte de Granite Rose, *S. fallax* was found on the carapace of spider crabs sold in the fish shop at Trebeurden in April 2003.

Castric-Fey (1996) reports *S. fallax* at Trebeurden-Ploumanac'h, probably the first indication of the presence of *S. fallax* in France, possibly dating back to 1993. At Perros Guirec in July 1998 several specimens were found on an abandoned lobster pot on the quay in the harbour. Castric-Fey et al. (2001) report it locally common in the archipelago of les Sept Isles, off Perros Guirec.

Farther east at Loguivy-de-la-mer, lobster pots showed a few *S. fallax* among a larger population of *Balanus perforatus*, but at Pors Even there were no *Solidobalanus fallax* on the pots, only *Balanus perforatus* and *Balanus crenatus*. At Erquy in the Bay of Saint Brieuc, in May 1998 and April 1999, *Solidobalanus fallax* was common but not abundant on fishing nets and lobster pots. It had been searched for in 1997 but was not found then.

In April 1999 *S. fallax* was common on one set of lobster pots (apparently from one fishing ground) at St Malo, but was not found on other sets of pots that may have come from different areas of the sea bed. It was not found at St Malo by Castric-Fey et al. (2001).

Southern North Sea

Specimens of *Solidobalanus fallax* on floating objects, including plastic, were washed up on the Belgian coast at Koksijde in 1996 and 1997 (Kerckhof, 1997a). *Solidobalanus* specimens settled on bamboo had been washed up near Oostende in the late 1980s, indicating earlier colonization (Kerckhof, 1997b). In most of the records for Belgium, *S. fallax* was accompanied by other warm water species, including *Balanus perforatus*, which is another barnacle that seems to be increasing in abundance in northern Europe (Herbert et al., 2003).

Several strandings of *S. fallax* were observed on the Belgian coast in 1998, the year showing the most numerous records. Only two strandings were recorded in 1999 and only one in 2000. The last finding dates from 15 June 2001, when a specimen with animal tissues was picked up on a plastic object on the beach between Oostende and Blankenberge. Since then there have been no additional records of *S. fallax* on Belgian and Dutch beaches, not even during spring and summer 2002 when there must have been a large influx of Atlantic water, as witnessed by strandings of *Velella velella* (L.). However, *Balanus perforatus* continued to be found on stranded objects. It seems that only in certain years do objects carrying *S. fallax* enter the North Sea, and this may indicate fluctuations in direction and origin of water flowing through the Channel.

There are surprisingly few records of *Solidobalanus fallax* from the Dutch coast. Faasse (1997) found dead specimens on the plastic entrances to a lobster pot washed up between Domburg and Westkapelle (Walcheren). The same author thinks there was an earlier finding in 1995 on plastic netting at Oostkapelle (also on Walcheren), but the material was not kept.

DISCUSSION

Solidobalanus fallax was previously recorded from a variety of biological substrata off north and west Africa, ranging from macroalgae to molluscs (Broch, 1927; Nilsson-Cantell, 1939; Stubbings, 1961a,b, 1963, 1965). The extreme depth range was from 15 to 220 m, but the species was most common at 30 to 80 m. While the species has been reported from Algeria, there have been no records from the rest of the Mediterranean (Relini, 1980). The new records from the Atlantic and Channel coasts help to define the distribution, but also point to the species being present in Europe nearly 50 years ago. Possibly it has become more abundant in recent years, with rising sea temperatures, and has thus become more easily detectable. Other warm water invertebrates have extended their range along the English Channel in the past two decades (Herbert et al., 2003; S.J. Hawkins, personal communication). Alternatively, the increasing prevalence of plastic discards in the sea has offered a greater opportunity for establishment, recognition and possible vectors for dispersal.

We can confirm that this barnacle does not settle on rocks (Southward, 1995). Off Plymouth and south-west England the live habitats known to be occupied are the upper valve of the queen scallop *Aequipecten opercularis*, the sea-fan *Eunicella verrucosa*, hydroids, the carapace of the spider crab *Maia squinado* and shells of *Buccinum undatum* inhabited by *Eupagurus bernhardus*.

The sea-fan *Eunicella verrucosa* appears to be a favoured substratum. The UK Marine Conservation Society

reported that, out of 1007 sea-fan colonies investigated during 2001/2002 in south-west Britain, only seven had barnacles attached (C. Wood, personal communication). However, in 2003, *Solidobalanus fallax* was very common on sea-fans off Plymouth with as many as 50% being infested, mostly near their bases, along the submerged cliff line off Plymouth Sound (see Table 2).

Plastic substrata on which *Solidobalanus fallax* has been found include synthetic netting/rope material, plastic coated metals, plastic pots and plastic bags. Either the cyprid larvae actively search for surfaces of this nature or else they fail to metamorphose on other substrata. Active selection of surface would imply the larvae have some means of detecting the 'energy' of the surface as proposed for other biofouling organisms (Gray et al., 2002). There has been much research in the past 20 years into the protection of ships and other structures from fouling by replacing toxic organometal paints with degradable coatings made from copolymers with low-energy surfaces (Christie & Dalley, 1987; Jacobson et al., 2003). This work assumes that barnacles and other fouling organisms select high-energy surfaces for settlement, as many of them appear to do. However, quite a few barnacles, including *Solidobalanus fallax*, do not always select high-energy surfaces. *Solidobalanus fallax*, *Balanus amphitrite*, *Balanus improvisus* Darwin and occasionally *Semibalanus balanoides* (L.), though not *Balanus spongicola*, will settle on polystyrene plastics (A.S. Elfimov and A.S. Clare, personal observations; Clare et al., 1994; Kawahara et al., 1999; Korn et al., 1999, 2001; Lagersson & Hoeg, 2002). There are quite a number of barnacle species that inhabit live cnidarian hosts.

The predilection shown by *Solidobalanus fallax* for biological surfaces can be compared to the choice by *Chelonibia* sp. of swimming crabs and turtles. *Chelonibia* spp. are rarely found on inanimate objects but can occur on wooden piling, which might be classed as a biological substratum (Frazier & Margaritoulis, 1990; A.J.S., personal observations). The use of biological substrata, especially motile life forms, can be regarded as an advantage, reducing predation and the risk of cover by sediment and possibly enhancing nutrition (cf. Achituv et al., 1997). The species of barnacles that use cnidarians as substrata will obviously gain protection from predation, though we should note that octocorals contain substances that inhibit settlement of *Balanus amphitrite* (Mary et al., 1991). Presumably, some species, including *Solidobalanus fallax*, are able to overcome cnidarian inhibitors. However, the initial settlement by *S. fallax* on *Eunicella verrucosa* is often at places where the coenenchyme has been damaged, exposing the 'skeleton'.

Biological substrata are ephemeral compared to rocks and stones. *Solidobalanus fallax* may compensate for this by rapid growth and maturation. The size-frequency of a sample from queen scallop shells (Figure 4A) shows two size-classes, the group of smaller specimens presumed to be from the previous autumn settlement, with only a few larger specimens surviving from preceding years. The size frequency of the plastic bag sample (Figure 4B) shows them all of one size-class, presumably having grown to 5 mm in seven months from settlement the previous autumn. The specimens found on the monofilament net in Anglesey were all of one size group, also probably settled the previous autumn. It seems likely that *S. fallax* is largely an annual species.

The attraction of *Solidobalanus fallax* to the pink sea-fan *Eunicella verrucosa* may adversely affect the condition and abundance of this UK Biodiversity Action Plan species which is also listed in Britain for protection under Schedule 5 of the Wildlife and Countryside Act 1981. Damage to the outer living coenenchyme of *E. verrucosa* can self-repair within a week or so (K.H., aquarium observations). However, if barnacles settle in that critical period when the skeleton is bare they are likely to prevent recovery, grow and, in turn, provide a substratum for other fouling organisms, including more *S. fallax*. The frequency of occurrence of *S. fallax* on *E. verrucosa*, off Plymouth at least, has increased significantly in the past two or three years and may be causing damage to sea-fan populations.

The increasing occurrence of *Solidobalanus fallax* along western European coasts means that it has the potential to become a serious pest of fish cages and other sea-farming structures to the south of Britain.

We are indebted to the masters and crews of the MBA vessels 'Squilla' and 'Sepia' for the dredge and trawl material. Thanks are due to members of the Belgian Strandwerkgroep (in particular Ingrid Jonckheere, Marie Thérèse Vanhaelen, Cédric d'Udecem d'Acoz and Hans De Blauwe) who assisted with the fieldwork and provided additional findings.

REFERENCES

Achituv, Y., Brickner, I. & Krez, J., 1997. Stable carbon isotope ratios in Red Sea barnacles (Cirripedia) as an indicator of their food source. *Marine Biology*, **130**, 243–247.

Broch, H., 1927. Studies on Moroccan cirripeds (Atlantic Coast). *Bulletin de la Société des Sciences Naturelles du Maroc*, **7**, 11–38.

Bullimore, B., Dyrynda, P.E.J. & Bowden, A., 1978. The effects of falling temperature on the fauna of Swansea Docks. *Progress in Underwater Science. Proceedings of the 11th Symposium of the Underwater Association at the British Museum (Natural History), 18–19 March 1977* (ed. J.C. Gamble and R.A. Yorke), pp. 135–146. Plymouth: Pentech.

Carriol, R.-P., 2001. Crustacés Cirripèdes actuels du Muséum d'Histoire naturelle de Lyon. *Cahiers Scientifiques du Muséum d'Histoire Naturelle de Lyon*, **2001**, 5–17.

Castric-Fey, A., 1996. Richesse et biodiversité en mer mégatidale: communautés sublittorale rocheuses de la région Trebeurden–Ploumanac'h (Nord Bretagne, France). *Cahiers de Biologie Marine*, **37**, 7–31.

Castric-Fey, A., Girard-Descatoire, A., L'Hardy-Halos, M.-Th. & Derrein-Courtel, S., 2001. *La vie sous-marine en Bretagne: découverte des fonds rocheux*. Association pour la découverte du monde sous-marin (Les cahiers naturalistes de Bretagne), 176 pp. Mèze, Biotope.

Christie, A.O. & Dalley, R., 1987. Barnacle fouling and prevention. *Crustacean Issues*, **5**, 419–433.

Clare, A.S., Freet, R.K. & McClary, M. Jr, 1994. On the antennular secretion of the cyprid of *Balanus amphitrite amphitrite* and its role as a settlement pheromone. *Journal of the Marine Biological Association of the United Kingdom*, **74**, 243–250.

Cooper, L.H.N., 1948. A submerged ancient cliff near Plymouth. *Nature, London*, **161**, 280–281.

Faasse, M., 1997. *Solidobalanus fallax* Broch 1927 aangespoeld in Nederland. *Het Zeepaarde*, **57**, 144–146.

Frazier, J.G. & Margaritoulis, D., 1990. The occurrence of the barnacle *Chelonibia patula* (Ranzani, 1818) on an inanimate substratum (Ciripedia, Thoracica). *Crustaceana*, **59**, 213–218.

Gray, N.L., Banta, W.C. & Loeb, G.I., 2002. Aquatic biofouling larvae respond to differences in the mechanical properties of the surface on which they settle. *Biofouling*, **18**, 269–273.

Herbert, R.J.H., Hawkins, S.J., Sheader, M. & Southward, A.J., 2003. Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **83**, 73–82.

Jacobson, A., Swain, G.W., Little, B. & Putnam, L., eds, 2003. Supplement 1, *Biofouling*, **19**, 1–205.

Kawahara, H., Tamura, R., Ajioka, S. & Shizuri, Y., 1999. Convenient assay for settlement inducing substances of barnacles. *Marine Biotechnology*, **1**, 98–101.

Kerckhof, F., 1997a. Waarnemingen van de Afrikaanse zeepok *Solidobalanus fallax* langs de Franse Atlantische kust en op drijvende voorwerpen aangespoeld op het Belgische strand. *De Strandvlo*, **17**, 34–44. [With English summary.]

Kerckhof, F., 1997b. *Solidobalanus fallax*: opmerkingen en aanvullingen. *De Strandvlo*, **17**, 62–64. [With English summary.]

Korn, M.O. & Elfimov, A.S., 1999. Larval development of a warm-water immigrant barnacle, *Solidobalanus fallax* (Cirripedia: Archaeobalanidae) reared in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 1039–1044.

Korn, M.O., Elfimov, A.S. & Skreptsova, N.V., 2001. Larval development of a barnacle, *Balanus spongicola* (Cirripedia: Balanidae) reared in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 775–779.

Lagersson, N.C. & Hoeg, J.T., 2002. Settlement behavior and antennulary biomechanics in cypris larvae of *Balanus amphitrite* (Crustacea: Thecostraca: Cirripedia). *Marine Biology*, **141**, 513–526.

Mary, V., Mary, A., Rittschof, D., Sarojini, R. & Nagabushanam, R., 1991. Compounds from octocorals that inhibit barnacle settlement: isolation and biological potency. In *Bioactive Compounds from Marine Organisms with Emphasis on the Indian Ocean, an Indo-United States Symposium* (ed. M.-F. Thompson et al.), pp. 331–339. Rotterdam: A.A. Balkema.

Nilsson-Cantell, C.A., 1939. Resultats scientifiques des croisières du navire-ecole Belge "Mercator". Cirripedia. *Memoirs du Museum Royaume d'Histoire Naturelle Belgique*, **15**, 91–94.

Relini, G., 1980. *Cirripedia Toracici*. Italy: Consiglio Nazionale di Richerche.

Southward, A.J., 1995. Occurrence in the English Channel of a warm-water cirripede, *Solidobalanus fallax*. *Journal of the Marine Biological Association of the United Kingdom*, **75**, 199–210.

Stubbings, H.G., 1961a. Cirripedia Thoracica from Tropical West Africa. *Scientific Results of the Danish Expedition to the coasts of Tropical West Africa (Atlantide Report)*, **6**, 7–41.

Stubbings, H.G., 1961b. Campagne de la *Calypso* dans le Golfe de Guinée et aux Iles Principe, Saõ Tome, Annobon (1956). Cirripedia. *Annales de l'Institut Oceanographique, Paris*, **39**, 179–192.

Stubbings, H.G., 1963. Cirripedia of the tropical south Atlantic coast of Africa. *Resultats Scientifiques. Expedition Oceanographique Belge dans les Eaux côtieres Africains de l'Atlantique Sud (1948–1949)*, **3**(10), 39 pp.

Stubbings, H.G., 1965. West African cirripedia in the collections of the Institut Francais d'Afrique Noir, Dakar, Senegal. *Bulletin de l'Institut Francais d'Afrique Noir*, series A, **27**, 876–907.

Stubbings, H.G., 1967. The cirriped fauna of tropical West Africa. *Bulletin of the British Museum (Natural History), Zoology*, **15**, 229–319.

Young, P.S., 1998. The Cirripedia (Crustacea) collected by the Fisheries Steamer "Meteor" in the Eastern Atlantic (1966–1975). *Arquivos Museo Nacional Rio de Janeiro*, **58**, 1–54.

Submitted 28 April 2004. Accepted 31 August 2004