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Chapter 1

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THE BIOLOGY OF *AUSTROMINIUS MODESTUS* (DARWIN) IN ITS NATIVE AND INVASIVE RANGE

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Abstract *Austrominius modestus,* formerly *Elminius modestus*, is a relatively small species of four-plated acorn barnacle, which is native to the subtropical and temperate zones of Australasia. It was introduced into Europe in the 1940s, where its current range includes England, Scotland, Wales, Ireland and continental Europe from Denmark to southern Portugal, as well as two reported locations in the Mediterranean Sea. This species occurs intertidally and subtidally on a very wide range of substrata in both its native and introduced range and is found on sheltered to intermediate exposed shores, but is absent from wave-exposed shores, probably due to the relative fragility of its shell. *A. modestus* is known to be both euryhaline and eurythermal, but its physiology (and that of other cirripedes) has been relatively little studied in comparison with other invertebrate species. Cold temperatures and competition from arctic-boreal barnacle species currently control its northern limit. At the southern limit, desiccation stress, or some other stress(es), may be limiting the abundance of *Austrominius modestus* by affecting cyprids and/or metamorphs at the settlement and recruitment stages. Abundance may also be limited by factors occurring at the reproductive stage. Since *Austrominius modestus* is an obligatory cross-fertiliser, the need for a critical breeding density is one of the factors that appears to have slowed the speed of its spread in Europe. Although this species can commence reproducing at a very young age and under optimal conditions produces multiple broods per year, its fecundity has not yet been studied. An examination of the age of first brooding, the timing and size and number of broods per year at sites at the northern (Scotland) and southern (Portugal) limits of the current invasive range of *Austrominius modestus* may provide a better understanding of the factors controlling its geographic distribution, abundance and speed of spread in its non-native range. For instance, warming waters could result in increased reproduction and recruitment of *Austrominius modestus*, leading to a reduced density of the native *Semibalanus balanoides* Linnaeus which may drive *Semibalanus balanoides* to extinction in certain parts of its range. Further research is necessary to determine the functional role of *Austrominius modestus* in relation to native species in order to understand the implications that changes in abundance and distribution of *A. modestus* may have for ecosystems.

Introduction

Austrominius modestus (Darwin 1854), formerly *Elminius modestus* Darwin (1854), is a species of barnacle, native to the subtropical and temperate zones of Australasia, that was introduced into Europe in the 1940s. While the spread of this species in its invasive range is well documented (e.g. Barnes & Barnes 1965b and subsequently), there has been little research regarding the ecology of this species. Research on the ecology of *Austrominius modestus* is timely because it may be an 'ecological sleeper' (Witte et al. 2010), with the potential for further increases in abundance accompanying predicted climate change, especially warmer air and seawater temperatures. A detailed understanding of the biology and ecology of *Austrominius modestus*, both in its native and introduced range, is necessary if we are to understand the causative factors controlling abundance changes in this species in the future and what implications these changes may have for ecosystems. Here we review what is known about the biology of *Austrominius modestus* in its native and invasive range and suggest key areas for future research. Each section of the review begins with a summary of the key findings before then describing them in detail.

Systematics

Subclass	Cirripedia Burmeister (1834)
Superorder	Thoracica Darwin (1854)
Order	Sessilia Lamarck (1818)
Superfamily	Tetraclitoidea Gruvel (1903)
Family	Austrobalanidae Newman & Ross (1976)
Subfamily	Elminiinae Foster (1982) (*nom correctum*, Buckeridge 1983)

Austrominius modestus (Darwin 1854).

Please see Buckeridge & Newman (2010) (Table 2 therein) for details of synonyms.

Description: Four symmetric wall plates usually tinged with slaty grey lines; plates thin but often with rounded ridges, giving the shell a sinuously octoradiate outline; basis membranous; tergo-scutal flaps of live specimens held flat, basically white, with brown marks at the pylorus and two blackish bands in the rostral half (Southward 2008) (see Plate 1).

Remarks: In young and uneroded specimens, each scutum carries a slaty grey line (Southward 2008). It is a small conical barnacle, measuring up to 10 mm in rostro-carinal diameter (RCD) when

Plate 1 Adult *Austrominius modestus* photographed at the new slipway in Bantry Harbour, south-west Ireland, by M.C. Gallagher.

fully grown, but specimens measuring up to 17 mm have been found under certain habitat conditions (Bishop 1954). *Austrominius modestus* does not possess pectinate setae on intermediate segments of cirrus III; the lack of this feeding development distinguishes it from other species of *Austrominius* (Buckeridge & Newman, 2010).

Knight-Jones & Waugh (1949) noted that Darwin (1854) suggested a close affinity between *Elminius*, *Tetraclita* and *Balanus*. *Elminius* is only distinguished from *Tetraclita* by the four compartments not being porose and by the basis being always membranous. Darwin considered *Tetraclita* closely allied to *Balanus* and could observe no difference in the animal's body, nor any constant difference in the opercular valves. According to Knight-Jones & Waugh (1949), the larval development of *Austrominius* confirmed that it was closely related to *Balanus*. However, when Pérez-Losada et al. (2014) undertook an extensive phylogenetic analysis of the familial relationships within the Balanomorpha, they found that neither *Austrominius modestus* nor *Elminius covertus* (*Austrominius covertus*) or *Elminius kingii* are closely related to *Balanus* species or *Semibalanus balanoides*.

There are five genera in the subfamily Elminiinae.

With four plates:

Austrominius Buckeridge (1983)	6 species
Elminius Leach (1825)	1 species
Matellionius Buckeridge (1983)	1 species
Protelminius Buckeridge & Newman (2010)	1 species

With six plates:

Hexaminius Foster (1982)	2 species

Distribution and zonation

Geographic distribution

Native range

Austrominius modestus is native to the subtropical and temperate zones of Australasia (see Figure 1), where it occurs in southern Australia and New Zealand (Buckeridge & Newman 2010). However, Flowerdew (1984), Foster (1982) and Foster & Anderson (1986) suggested the possibility that *Austrominius modestus* may have been introduced to southern Australian ports from New Zealand by shipping, pre-1836, when Darwin recorded it on oysters in Sydney Harbour (Darwin 1854). However, *Austrominius modestus* is not listed by Jones (2012) as one of the 16 barnacle species introduced into Australia. Moore (1944) and Foster (1978) showed maps of its distribution around New Zealand, relative to three and six other species of acorn barnacle species, respectively. While Bishop (1951) described *Austrominius modestus* as one of the most geographically confined of all barnacles (i.e. this species is only found in New Zealand and arguably in Australia), it is abundant. For instance, Hutton (1879) recorded *Austrominius modestus* as abundant on rocks in New Zealand, and this barnacle species is the most common fouling barnacle in New Zealand harbours (Foster 1982). In suitable habitats within New Zealand (see 'Horizontal and vertical zonation' subsequently), this barnacle species occurs in the North and South Islands, as well as Stewart Island. *Austrominius modestus* has not been recorded or collected from the Kermadec Islands or from the islands to the south of Stewart Island, New Zealand (Foster 1967a, 1978). Foster (1978) questioned whether *Austrominius modestus* occurs in Chatham Island, New Zealand, as Young (1929) recorded it

Figure 1 The current known distribution of *Austrominius modestus* in Australasia (green) and where introduced into Europe (red). (Drawn by M.C. Gallagher.)

there, but Knox (1963) stated that it was absent. In its proposed introduced range within Australia, *Austrominius modestus* occurs in South Australia, New South Wales, Tasmania and Victoria (e.g. Darwin 1854, Hutton 1879, Hoek 1883, Gruvel 1905, Jennings 1918, Nilsson-Cantell 1926, Moore 1944, Womersley & Edmonds 1958, Foster 1967a, 1978, 1982, Leslie 1968, Thomas & Edmonds 1979, Hutchings & Recher 1982, Keough 1983, Bayliss 1988, Jones 1990, Jones et al. 1990) but is apparently not present much north of Port Jackson (Pope 1945). *Austrominius modestus* is one of 279 barnacle species recorded in Australian waters but one of only six that have an Australasian distribution (Jones 2012).

Current invaded distribution

Austrominius modestus was introduced into Europe in the 1940s. Outside Australasia, Buckeridge & Newman (2010) described the distribution of *Austrominius modestus* as introduced and naturalised in Great Britain (including the Shetland Islands) [Ireland] and Western Europe and arguably naturalised in the Mediterranean (Bassin de Thau, near Marseilles). On the European continent, its current (2018) range is believed to be as described by Southward (2008), that is, from Denmark to southern Portugal (see Figure 1), but please see details of historical records in 'Changes in its distribution in its non-native range'. The first published record of *Austrominius modestus* in Europe was from Chichester Harbour in 1945 (Bishop 1947), but it is now known to have been present before 1945. This species was possibly transported to Britain via ship or flying boat (Bishop 1947, Crisp 1958). Since its introduction to Europe in the 1940s, *Austrominius modestus* has become widespread on European Atlantic shorelines (Harms 1999, Tøttrup et al. 2010) (see details in 'Changes in its distribution in its non-native range'). In Europe, *Austrominius modestus* was thought to be the only species within the Subfamily Elminiinae that successfully colonized outside its native range. Egan & Anderson (1985) cast doubt on this due to some anomalies (please see 'Larval Stages' subsequently regarding a possible explanation for these) when they compared larvae of the Australasian species with larval descriptions of European species. However, Foster & Anderson (1986) suggested subsequently that all European studies on the biology and ecology of *Elminius* refer to *Austrominius modestus*. Furthermore, Buckeridge & Newman (2010) do not list any other species of the Subfamily Elminiinae being introduced into Europe, although *Elminius kingii* has been introduced from South America to eastern Canada (Gollasch 2002). Following Barnes (1989), we have used *Austrominius modestus* for all of the European publications, except in direct quotes. Buckeridge & Newman (2010) mentioned a record of *Austrominius modestus* from the Azores but noted that it is of "questionable identification". Southward (1998) indicated that this record was more likely to be a juvenile of *Chthamalus stellatus* with plate abnormalities (Southward pers. comm. to R. O'Riordan). Torres et al. (2012) also suggested that this specimen was probably misclassified. The only known published record of *Austrominius modestus* in South Africa is of a single individual in 1949 (Sandison 1950), and it has not been recorded there subsequently and is assumed to have failed to colonize there (Barnes 1989, Buckeridge & Newman 2010). Kerckhof (2002) suggested that *Austrominius modestus* had spread to Japan but provided no reference to this record.

Several publications, such as, for Australasia, Foster (1982), Bayliss (1988, 1994), Jones (1990) and Buckeridge & Newman (2010) and Southward (2008) for its introduced range, provide details on how to distinguish *Austrominius modestus* from other species of adult barnacles.

Horizontal and vertical zonation

In both its native and introduced range, *Austrominius modestus* attaches to a wide range of substrata and occurs intertidally and subtidally. Although *Austrominius modestus* can be found at higher shore levels, greater densities occupy middle and lower levels. *Austrominius modestus* is found on sheltered to intermediate exposed shores in habitats including rocky shores, estuaries, mangroves, harbours and ports but is absent from the most wave-exposed shores, probably due to the relative fragility of its shell.

Australasia In New Zealand, *Austrominius modestus* is the species of barnacle that penetrates furthest into harbours and estuaries and is common in mangrove forest and eelgrass beds (i.e. *Zostera*), occurring more often in sheltered locations on open coasts with clean water. However, *Austrominius modestus* withstands only moderate wave action and is absent from the most exposed stretches of rocky coasts (Moore 1944). Foster (1978) commented that it was not surprising that *Austrominius modestus* occupies habitats that are not prone to severe wave action. This is due to certain features of its shell, which is weakly constructed but solidly calcareous, with narrow radii that abut onto the adjacent parietes only basally (Foster 1978). Although *Austrominius modestus* cannot tolerate wave-exposed shores, it can grow well in strong currents in more sheltered habitats, for example, in its native range at the edge of channels in mangrove forests, where the current is fast (Moore 1944). An ability to thrive in very fast currents has also been seen in its introduced range in drowned river valleys in northern France, where they can reach larger sizes than reported elsewhere (see details in 'Size, growth rate and age' subsequently).

Austrominius modestus is fairly versatile with respect to tidal level (Moore 1944), and it has been recorded on a wide range of substrata in the midlittoral and shallow sublittoral zones (Moore 1944, Morton & Miller 1968, Foster 1978, Jones 1990). Gruvel (1905) noted that it occurred attached to rocks in the littoral as well as attached to shellfish and was often associated with *Balanus trigonus* and *Balanus vestitus*. In Australasia, the main level that it occurs at intertidally is the middle shore, reaching high abundances. Similar abundances can be found in slight shade on wharf piles or under mangroves (Moore 1944). However, it can be found higher up the shore, above other species, where fresh or brackish water seeps over a rock or where there is a damp shaded ledge (Moore 1944). Foster (1978) noted that on sheltered shores in its native range, it can reach as far up as the high water of neap tides. According to Davey (last accessed, 2018), on southern Australian shores, it shows a preference for higher shore levels, where it might be only covered for a few hours each month. Unlike other belt-forming intertidal barnacles, *Austrominius modestus* grows not only on the upper rock and other surfaces but also on the underside of stable boulders (Moore 1944), which, as Foster (1978) had noted, is a desiccation-protected habitat. Where *Austrominius modestus* occurs on horizontal surfaces, this species may be protected from desiccation by a layer of silt, sometimes with small algae. Clean vertical rock, facing the sun, is unfavourable due to the lack of protection from desiccation (Foster 1978). With respect to its lower limit, *Austrominius modestus* has been collected on mussels from a depth of 3.7 m and on test panels down to about 5 m (Jones 1990). *Austrominius modestus* survives well on sublittoral surfaces, including ships' hulls (Foster 1967a). This fouling proclivity enabled *Austrominius modestus* to overcome oceanic barriers and become sympatric with related species in Australia and Europe (Foster 1978). Along with *Austrominius modestus*, *Amphitrite amphitrite* and *Balanus trigonus* are frequent fouling species on boats in the north of New Zealand (Foster 1967a), and all three species are now known in European waters (Southward 2008). In 1946, all three species were found together in Liverpool on the hull of a ship that had been in southern Australia and New Zealand, which had journeyed for 30 days through the freshwater conditions of the Panama Canal (Bishop 1947) (see 'Salinity tolerances' subsequently).

Europe In Europe, *Austrominius modestus* is typically found in sheltered waters, including estuaries, harbours, bays and sea lochs, rather than on wave-exposed coastlines (e.g. Southward 1955b, Crisp 1958, Crisp & Fischer-Piette 1959, Barnes & Barnes 1961, Foster 1971b, Gomes-Filho et al. 2010, Gallagher et al. 2017). *Austrominius modestus* was not found in quadrats at the most wave-exposed sites studied in Plymouth, England (Burrows 1988), and Lough Hyne, west Cork, Ireland (O'Riordan 1992). *Austrominius modestus* in its native waters appears to occupy the position held by *Amphibalanus improvisus* in British waters (Bishop 1947). In their 1954–1956 survey, Crisp & Southward (1958) noted that *Austrominius modestus* had already replaced *Amphibalanus improvisus* in many of its habitats in England. By 2003, estuaries in south-west England were dominated by *Austrominius modestus*, accompanied by *Amphibalanus improvisus* and *Balanus crenatus* at low tide levels, with all three occurring intertidally (Ross et al. 2003). The latter authors also reported *Austrominius modestus* at low densities on shores of moderate wave exposure, with normal salinities, but it was outnumbered by three native species of barnacles at all shore heights in the intertidal. Southward (1958) had described the normal zonation of *Austrominius modestus* in Great Britain as midlittoral and infralittoral, mean high water neap (MHWN) to shallow water. At Warwick Bay, Dale, Pembrokeshire, adults were found as high ~5.4 m above chart datum (CD) there, but maximum densities (of adults and spat) were seen at ~2.7 m above CD (Moyse & Knight-Jones 1967). Foster (1971b) commented that on shores where these barnacles co-occurred, without the modifying effect of wave action, *Austrominius modestus* could survive 30–60 cm higher than *Semibalanus balanoides*. Foster (1987) described *Austrominius modestus* as biologically competent in shallow seas, and it was recorded sublittorally in Great Britain down to a depth of about 5 m below low water spring (Crisp 1958), which is similar to its depth in Australasia, as well as occurring on sublittoral panels (e.g. Crisp & Davies 1955). In the early years of its spread to continental Europe, Hartog (1953) said it behaved as an intertidal species, with only a few specimens below water mark on Dutch shores, which was the same situation recorded by Wolf (1973) in the Dutch Wadden Sea. At Cuxhaven, in the Elbe estuary, Kühl (1954, Figure 2, p. 55) showed *Austrominius modestus* occurring from about 3 m (co-occurring there with *Amphibalanus improvisus* and *Mytilus* mussels) to 6 m (just below MHW), where it was the only barnacle species, having co-occurred with *Semibalanus balanoides* (and *Mytilus*) from about 3.3–4.3 m above CD. However, *Austrominius modestus* was subsequently recorded sublittorally in a number of areas in the North Sea (e.g. Anger 1978, Harms & Anger 1983). It has been reported to have been found in the Northern Adriatic Sea, Italy, at a depth of 22–24 m (Casellato et al. 2007), but this record does not appear in national reports of the International Council for the Exploration of the Sea Working Group on Introductions and

Tranfers of Marine Organisms (ICES WGITMO), and this is much deeper than it has been found elsewhere. Kerckhof (2002) said that *Austrominius modestus* was the most common barnacle of Belgian fauna, including dominating most of the offshore buoys (Kerckhof & Cattrijsse 2002), but sublittoral offshore substrata were not colonized by *A. modestus*, remaining the exclusive habitat of *Balanus crenatus*. In the sublittoral zone in Ireland, *Austrominius modestus* has been recorded occurring with *Balanus crenatus* (O'Riordan 1967), as well as with other sublittoral species on plates down to a depth of 12 m (Watson et al. 2005). Southward (2008) noted that, in the sublittoral, specimens of *Austrominius modestus* and *Balanus crenatus* may be found co-occurring. He warned that sometimes *A. modestus* resembles *B. crenatus* and needs to be cleaned of any epizoic growth to confirm identity. Barnes et al. (1972) also pointed out that, where there is sand scour (e.g. Hossegor, France), erosion can cause the specimens to be mistaken as *Amphibalanus improvisus* or *Amphibalanus eburneus*.

Physiology and function

Over 20 years ago, Anderson (1994) pointed out that surprisingly little research had been carried out on the physiology of cirripedes, despite their diversity, widespread availability and ecological importance, although there has been some research undertaken more recently on a few species of barnacle (e.g. Wrange et al. 2014). With respect to *Austrominius modestus*, research has focussed on this species's tolerances to temperatures and salinities and the effects of these environmental parameters on cirral activity and metabolism during various stages in its life cycle. The small amount of research to date on its endocrinology looked at the processes and substances controlling hatching, larval metamorphosis and moulting, while its shell structure and growth under different conditions have also been examined. Subsequently we summarise what is known about *Austrominius modestus*, most of which is based on the species in its introduced range in Great Britain (England, Scotland and Wales).

Cirral activity and metabolism

Austrominius modestus has a faster cirral beating rate than most other species in British waters (Crisp & Davies 1955), including *Semibalanus balanoides* (Southward 1955a). This cirral activity can occur over a wider range of temperatures, affecting both its feeding and respiration, when immersed. Adult thoracican barnacles use their cirri to filter food from the water and gather oxygen, so the rate of beating of these cirri reflects the general metabolic rate of a barnacle (Southward 1955a, Crisp & Southward 1961). For maximum growth, *Austrominius modestus* needs a high concentration of suspended material (Crisp & Davies 1955), which is characteristic of rich inshore waters (Crisp 1964a). *Austrominius modestus* is one of the barnacle species that can show both normal and fast (accelerated) beating of the cirri, but fast beat planktivory is the most usual/dominant feeding mode of this species (Crisp & Southward 1961, Anderson & Southward 1987). This mode of feeding is also seen in at least two other members of the Subfamily Elminiinae (Anderson unpublished, cited in Anderson & Southward 1987). Anderson & Southward (1987) mentioned further unpublished research by Alan Southward on the cirral activity of *Austrominius modestus*. Using milk trails and carmine suspensions, he showed that this fast beat can generate a water flow that is at least twice as wide as the spread cirral net and extends at least three shell diameters each way along the rostro-carinal axis. Fast beating therefore greatly increases the flow of particles nearby, which benefits species such as *Austrominius modestus* when it occurs in sheltered waters. The fast beat is best seen in medium and small *Austrominius modestus* and in laboratory temperatures is extremely fast (Anderson & Southward 1987). Southward (1955b) reported a significantly higher mean frequency of cirral beating in less than one-year-old *Austrominius modestus* collected from the mean low water neap (MLWN) than MHWN in Plymouth. According to Crisp & Patel (1961), the usual activity in *Semibalanus balanoides,* a species with which it may compete, at least at the northern limits of its introduced range (see subsequently), is the normal beat. In comparison to *Semibalanus balanoides*, *Austrominius modestus* has relatively longer cirri, with a few more segments (Crisp & Maclean 1990). However, Crisp & Maclean (1990) warned that the number of segments in each cirrus cannot be used as a taxonomic character because the number of segments increases with animal size, but the equation describing the relation between segment number and animal size may well be diagnostic. Southward (1965) had mentioned that certain physiological data, such as cirral activity rather than cirral size, can be of use in the taxonomy of barnacles but emphasised the need for systematic exactness in physiological work. Moore (1944) described the cirral structure of *Austrominius modestus* in detail, and Jones (1990) provided cirral counts.

Southward (1955a) examined how cirral activity, which may affect both feeding and respiration, varied with temperature in the laboratory. He found that *A. modestus* was active at lower and higher temperatures than native southern and northern species, respectively, while it was active at a wider range of temperatures than *Balanus crenatus*, which occurs, like *A. modestus*, in sheltered conditions. *A. modestus* showed a much greater frequency of cirral beating (17–18 beats/10 seconds at 20°C) than the five native species tested (Southward 1957). Feeding of *Austrominius modestus* ceased at temperatures below 2.5°C and above 32.5°C. A maximum of 22 beats/10 seconds occurred at 24°C.

Southward (1955a) pointed out that it would be interesting to know the range of cirral activity of *Austrominius modestus* in Australasia, since the lower temperatures tolerated by the British-bred specimens are lower than the lowest (7°C) monthly mean seawater temperatures there, suggesting that *A. modestus* has acclimatised to European conditions (see also Southward 1964). However, Ritz & Foster (1968) noted that air and seawater temperatures in its native range may be as low as 0°C and 4°C, respectively. Patel & Crisp (1960b) reported that the rate of cirral beating of *Austrominius modestus* prior to collection was much faster than that of the other three barnacle species tested. The ambient mean seawater temperature in the relatively cool waters of North Wales in the four weeks prior to collection was 12°C. In the laboratory, Crisp & Ritz (1967) acclimated *Austrominius modestus* for five months at 4, 15 and 25°C and then examined the activity patterns (cirral beating) over five hours in either 3–4, 14–15, 21–22 or 30–31°C. They found that below the temperature of maximum frequency of beating, the animals that had been acclimated at the lowest temperature showed the highest rate of cirral beat. The temperature of the maximum rate of beating and the upper limit of activity increased as the acclimation temperature increased. They noted that the acclimation half-time was found to be on the order of 5–10 days in *Austrominius modestus*. They also examined the influence of temperature on the rate of normal and fast beating in fed *Austrominius modestus* before and after seven months acclimation to three temperatures, as well as the effect of starving. They reported that prolonged starvation at the higher temperatures eventually resulted in a lowered rate of cirral beating.

Anderson (1994) described barnacle digestion, while a number of authors have calculated the ingestion rate of *Austrominius modestus*. Crisp (1964a) gave a value of 0.6 mg tissue dry wt d^{-1}, for a barnacle with a RCD of 10 mm (at 13–17°C). According to Rainbow & Wang (2001), the dry weight of this sized barnacle would be 1.37 mg, giving a value of 0.44 g $g^{-1}d^{-1}$. Using the filtration rate of 11.4 ml hr^{-1} per individual, suggested by Crisp & Southward (1961), and assuming a typical seston concentration of 2 mg l^{-1} in the sea, Rainbow & Wang (2001) calculated an ingestion rate of 0.55 mg d^{-1} or 0.40 g $g^{-1}d^{-1}$ for a barnacle of 1.37 mg tissue dry weight.

Emersion, oxygen uptake, anaerobic metabolism and lactic-acid production

Similar to other intertidal barnacle species, adult *Austrominius modestus* utilize the pneumostome to use atmospheric oxygen for respiration during emersion, forming lactic acid under anoxic conditions and in emersion. The use of a pneumostome subjects the mantle cavity minimally to the atmosphere (Barnes & Barnes 1957, Barnes et al. 1963, Grainger & Newell 1965, Crisp & Ritz 1968, Foster 1970). However, the oxygen consumption when emersed is much lower than when immmersed (Grainger & Newell 1965). Since the water that is lost from the mantle cavity is replaced by air bubbles, the mantle cavity can fill with air (Davenport & Irwin 2003). *Austrominius modestus* and *Semibalanus balanoides* usually use up the oxygen in these bubbles within two–three hours and do not regain oxic conditions until re-immersed in seawater, but in *Chthamalus stellatus*, the air bubble is repeatedly refreshed for many hours by pneumostome formation. However, in response to low environmental salinity, all three barnacle species close their opercular plates firmly and rapidly use up oxygen within the mantle fluid. A similar valve closure occurs during extensive desiccation, when they use energy derived from anaerobic metabolism (Barnes & Barnes 1964, Hammen 1972). Barnes et al. (1963) found that three species of European barnacles formed lactic acid under anoxic conditions and in emersion. Boulton et al. (1967), who were studying the metabolic pathways in *Austrominius modestus* in order to understand the biochemical mechanisms by which toxic compounds in antifouling substances could affect this species (see 'Pollution' subsequently), found only very minor incorporation of labelled substrates into lactic acid of *A. modestus*. They mention previous research by Munday & Walker (unpublished), demonstrating the operation of several enzymes of the glycolytic and tricarboxylic acid cycle pathways in adult *Austrominius modestus*.

Little has been reported about the respiration rates of adult *Austrominius modestus*, but CO_2 fluxes due to respiration (and calcification; see subsequently) ranged from 3.6 ± 0.84 to 14.1 ± 3.63 $\text{mol}_{CO2}\ m^{-2}\ year^{-1}$ in intertidal specimens at two sites in France (Golléty et al. 2008). Bhatnagar & Crisp (1965) examined the oxygen consumption, as measured by respirometry, of stage II nauplii of *Austrominius modestus*. With a dry organic weight of 0.38×10^{-6} g, the actual oxygen uptake was 2.2×10^{-6} ml O_2 per hour, giving a weight-specific oxygen uptake of 5.8 (ml O_2 hr^{-1} g [dry weight]). Similar levels of oxygen uptake occur in *Austrominius modestus* nauplii as in other invertebrate planktotrophic larvae (Crisp 1976).

Temperature

Austrominius modestus is eurythermal (Barnes & Barnes 1966), tolerating temperatures ranging from approximately –5°C up to 48°C in experimental conditions. The distribution of *Austrominius modestus* in its native New Zealand suggested that it is a temperate to warm-water species (Foster 1969), since the water temperature range in the subtropical and temperate parts of New Zealand varies between 4 and 21°C (Ritz & Foster 1968) but can reach 24°C (Harms & Anger 1989), and air temperatures may reach 40°C (Foster 1969) (compared to >30°C in Plymouth, Great Britain [Southward 1958]), while air temperatures in the south of New Zealand seldom go below 0°C (see Figure 8 and references cited by Harms & Anger 1989). In its invasive range, *Austrominius modestus* tolerates higher temperatures than the arctic-boreal *Semibalanus balanoides* (Southward 1958). However, it is not as tolerant as warm-water species, such as '*Chthamalus stellatus*', which has a very high upper temperature limit, which is in line with the latter's tropic-Mediterranean centre of distribution (Foster 1969). Please note that '*Chthamalus stellatus*' is used for research predating Southward's (1976) separation of '*Chthamalus stellatus*' into *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward. In Europe, *Austrominius modestus* cannot tolerate as low temperatures as arctic-boreal species, for example, *Semibalanus balanoides*. Hence, cold temperatures and competition from arctic-boreal barnacle species are believed to affect its current northern limit as well as historic invasive range in Europe. Unusually cold winters in Europe are believed to have delayed extensions northwards (in 1946 and 1947) and resulted in greater mortality in Ireland of *Austrominius modestus* than native barnacle species (in late 2009 and 2010). In contrast, mild winters and warmer-than-normal summers allow increases in its abundance there.

Effect of high temperatures and variation with season and life stage

Although thoracican barnacles can tolerate high temperatures, this varies among species and intraspecifically with age, season and habitat. Southward (1955a) reported that heat coma in adult *Austrominius modestus* (loss of irritability – when normal reaction to touch, namely a closing of the terga and scuta, failed to occur) occurred at 36–38°C. However, subsequent research established that the upper lethal temperature (ULT) of adult *A. modestus* from British waters was between 48.0–48.3°C and 44.2–44.8°C (for 50% mortality with a heating rate of 1°C min^{-1} and 2°C min^{-1}, respectively) (Southward 1958, Crisp 1968, Foster 1969). Southward (1965) reported that *Austrominius modestus* collected from English shores showed 50% mortality after 7 h 30 min at 37°C, but only 5 h 15 min at 40°C. In comparison, '*Chthamalus stellatus*' could survive for 29–30 hours at 40°C and 30 minutes at 50°C. Southward (1958) found that *Austrominius modestus* was more resistant to high temperatures than *Semibalanus balanoides* and *Perforatus perforatus*. This allows it to occur at higher levels on the shore than the two latter species. Foster (1969) suggested that 50% mortality would occur in *Semibalanus balanoides* and *Austrominius modestus* at temperatures of 36°C and 38°C, respectively, at mid-tide levels on shores with semi-diurnal tides, if maintained for a full 6 hours. Foster (1971b) reported on the water loss and mortality of *Austrominius modestus* on pier piles at Menai Bridge. After two weeks of unusually fine weather in June 1969, coincident with neap tides and above-normal temperatures, he found that some of those occurring highest on the pier piles were quite dry and shrivelled and it was not possible to extract blood from the organisms. Younger (spat) and smaller (up to 4 mm) *Austrominius modestus* were particularly affected.

High temperature tolerances may not vary seasonally for subtidally occurring barnacles, but species which live in the intertidal may show variation with season. For example, when Foster (1969) tested barnacle species collected in Great Britain in summer (July) and winter (February) for high temperature tolerance, continuously submerged adults of *Austrominius modestus* (and *Balanus crenatus*) showed no seasonal change in high temperature tolerance. However, intertidal arctic-boreal *Semibalanus balanoides* were more susceptible to prolonged high temperatures in the winter.

At the southern invasive limit of *Austrominius modestus* in Europe, desiccation stress, or some other stress(es), may be limiting the abundance of *A. modestus* by affecting cyprids and/or metamorphs at the settlement and recruitment stages. When emersed, barnacles in the intertidal may have to survive both high temperatures and resist desiccation (Foster 1969). Although temperature tolerance is independent of size (Foster 1971b), the length of time that barnacles survive under desiccation stress is dependent on the size of the individual. Desiccation results from the combined effect of temperature, humidity and wind speed (Foster 1971a). When Foster (1971a) examined the median lethal time (h) for barnacles, measuring a range of rostro-carinal diameters at different temperatures and humidity, he found that smaller *Austrominius modestus* (and *Balanus crenatus* and *Semibalanus balanoides*) were more susceptible to desiccation at normal temperatures and low humidities than larger barnacles. When individuals of about the same size were compared, the lower shore *Balanus crenatus* was much more susceptible to desiccation and lost water more quickly than the other two species, which lost water at similar rates, but *Semibalanus balanoides* survived slightly longer than the same-sized specimens of *Austrominius modestus*. Foster (1971a) noted that high intertidal '*Chthamalus stellatus*', which survived longest in emersion, appeared to be relatively impermeable. For barnacles of the same volume and at 0% relative humidity, the mean lethal time for spat (at 18°C) and adults (at 19°C) was much shorter in *Austrominius modestus* (spat = 7 h, adults = 46 h) than in '*Chthamalus stellatus*' (spat = 48 h, adults = 165 h). Although *Austrominius modestus* is slightly more tolerant of high temperatures and *Semibalanus balanoides* appears to tolerate slightly greater tissue dehydration (which may be linked with to greater tolerance of cold), Foster (1971b) wrote that it is unsurprising that these two species occupy similar intertidal stations. Foster's (1971b) research on salinity and desiccation is discussed subsequently. Cawthorne (1979) investigated the high temperature tolerances of newly released nauplii of *Austrominius* *modestus* and *Semibalanus balanoides* to sinusoidal, abrupt or steady-state changes. For both species, the sinusoidal regime was tolerated best and allowed survival to maximum temperatures, but *Austrominius modestus* nauplii were significantly more tolerant of cyclic exposure to high temperatures (Cawthorne 1980).

When discussing the spread of *Austrominius modestus* to more southerly shores on European coasts, Foster (1971a) noted that *A. modestus* may survive better under warmer and, presumably, drier environments, in comparison to *Semibalanus balanoides*. Foster (1969) and Southward (1958) concluded that the temperature tolerances were linked to the temperatures in the geographical distribution and vertical zonation of these barnacle species (see 'Horizontal and vertical zonation' previously). In its native range, *Austrominius modestus* shows considerable resistance to desiccation, with some specimens attached to a mangrove leaf showing active feeding when placed in fresh water. This is despite having been left on a sunny laboratory bench for ten days without water (Moore 1944). However, *Austrominius modestus* does not tolerate too much direct sunlight (Moore 1944, Knight-Jones & Stevenson 1950), with, as mentioned previously, vertical rock facing the sun being unfavourable (Moore 1944). Similarly, Foster (1987) pointed out that the densest populations of *Austrominius modestus*, along with another member of the Subfamily Elminiinae, *Austrominius covertus*, occurred where there was some protection from direct insolation.

Effect of low temperatures

Thoracican barnacles can survive temperatures below 0°C, but this varies with species, season and whether the species is living in the intertidal or subtidal. Southward (1955a) had reported that chill coma occurred at 0°C in *Austrominius modestus*, but Crisp & Davies (1955) noted that at Burnham-on-Crouch, south-east England, *A. modestus* could survive at temperatures well below 0°C, but they may have been referring to subtidal, rather than intertidal, specimens. At −5.0°C (but not at −10.0°C), *Austrominius modestus* was less tolerant than the native *Semibalanus balanoides* and '*Chthamalus stellatus*' (Southward 1958). After 18 h, 50% mortality of *Austrominius modestus* occurred at −4.3°C in the summer and −6.0°C in the winter, while for *Semibalanus balanoides*, the respective temperatures were −6.0°C and −16.0°C (Crisp & Ritz 1967, Ritz 1967). Ritz (1967) and Tooke & Holland (1985) commented that *S. balanoides* had greatly enhanced cold tolerance in the winter (lower mean lethal temperature range of −17.3 to −19.2°C in winter vs −7.0 to −8.2°C in summer), but *Austrominius modestus* showed little seasonal variation (mean lethal temperature range of −4.9 to −6.7°C in winter vs −5.1 to −6.3°C in summer). Southward (1958) commented that the relatively low resistance of *Austrominius modestus* to cold temperatures was surprising considering its abundance at that time on the cold east coast of England. However, after the unusually cold winter of 1962/63, only 50%–80% mortality of *Austrominius modestus* occurred, in comparison to 100% mortality in some molluscan species, in the intertidal zone in south and south-east England (Crisp 1964a). It was thus suggested that *Austrominius modestus*, along with *Semibalanus balanoides* and '*Chthamalus stellatus*', which are subjected to desiccation by evaporation in summer, may be pre-adapted to withstand the effects of dehydration of the tissue fluids by freezing in winter (Crisp 1946). In the laboratory, Tooke & Holland (1985) found very similar phospholipid fatty acid composition in samples from Great Britain, which they thought might reflect the similarity of their physical environment and diet. However they did find changes in sphingomyelin (essentially confined to the plasma membrane) between winter (January) and summer (August). In *Austrominius modestus*, there was an increase and decrease in levels of monounsaturated fatty acids and saturated fatty acids, respectively, going from winter to summer. The differences in the ability of *Austrominius modestus* and *Semibalanus balanoides* to acquire freezing tolerance may be related to seasonal changes in total phospholipid fatty acid of the plasma membrane (Tooke et al. 1985). At Lough Hyne Marine Nature Reserve (LHMNR), southwest Ireland, *Austrominius modestus* was found to experience higher levels of mortality than native barnacle species during the cold winters of 2009/2010 and 2010/2011 (Gallagher et al. 2017). In The Netherlands, although *Austrominius modestus* survived the cold and protracted winter of 1946–1947, this abnormally cold winter delayed its spread. Based on laboratory and field research at Helgoland, Germany, it was suggested that extreme winters may act as a strong factor in genetic selection towards cold temperature adaptation in these populations of *Austrominius modestus*, which are towards their current northerly continental European invasive limits (Harms 1986, Harms & Anger 1989). Temperatures during such extreme winters may drop to less than −20°C on single days and caused mortality there of most of the adult intertidal *Austrominius modestus* and ca. 70% of subtidal *A. modestus* (Harms & Anger 1989). Kühl (1963) suggested that *Austrominius modestus* was more sensitive to low winter temperatures than some of the native species in the Elbe estuary, resulting in high winter mortality of the former species. However, when air temperatures drop below normal winter ones, they survive in the tidal zone of Helgoland or Borkum. Theisen (1980) attributed the disappearance over winter of *A. modestus* from an intertidal area in Danish waters to a severe winter. In December 1978, over 70% of the intertidal barnacle population at their site consisted of *Austrominius modestus*, but no living specimens could be found intertidally the following March or October (although they noted that they may have survived subtidally). Jensen & Knudsen (2005) had suggested that they were not able to establish themselves in the Danish Wadden Sea because of the borderline low temperatures. This results in them dying during cold winters, due to ice formation, but repopulating during milder ones. However, Witte et al. (2010) has described, towards its northern introduced range, the impact of a series of mild winters and warm summers. Barnes & Barnes (1966) noted that it only started to increase in abundance in the Clyde estuary in Scotland after a warmer summer than normal, in 1959.

Salinity

Austrominius modestus has been described as extremely euryhaline (e.g. Southward 1955a, Barnes & Barnes 1974) and hardy (Knight-Jones 1948). This tolerance to a wide range of salinity allows *Austrominius modestus* to occupy fully marine habitats, but also those that are characterised by lower and higher salinities. In its native range, in Australasia, this species is able to penetrate deep into estuaries and harbours, since it can tolerate brackish and muddy waters, including mangroves. Darwin (1854) recorded *Austrominius modestus* on oysters in Sydney Harbour, in a lagoon, which was almost separated from the sea. Jones (1990) noted its tolerance to reduced salinities, although Foster (1987) suggested that these conditions were rather unfavourable to barnacles. In Europe, salinity fluctuations have been found to affect its distribution within estuaries (see e.g. Wolf 1983, Attrill & Thomas 1996, Gomes-Filho et al. 2010), but it is able to extend further into estuaries than the native *Semibalanus balanoides* (Foster 1970, 1971b).

The embryos of *Austrominius modestus* can develop at salinities between 15–20 and 40, which is similar to other thoracican barnacle species tested (Barnes & Barnes 1974), but the nauplii of *A. modestus* can be slightly more tolerant to lower salinities than the other species (Bhatnagar & Crisp 1965). Crisp & Costlow (1963) pointed out, that by living in estuaries, the adults of *Austrominius modestus* experience very low salinities periodically. Since egg masses are permeable to salts, they may be subjected to the same salinities as the adults. Barnes & Barnes (1974) subsequently examined the responses of the embryos of six species of thoracican barnacles, including *Austrominius modestus*, to hypo- and hypersaline media in the laboratory. Regardless of what stage of development the cultures were started, the range of salinity over which the embryos would develop, to give free-swimming stage I naupliar larvae, was similar in all species, irrespective of their known habitat preferences. Each species was investigated at a single temperature only, which was 20°C for *Austrominius modestus* and at a salinity of 16. Embryos which had already developed segments and appendages continued to develop and were successfully reared to hatching, however this did not occur in embryos that were at earlier stages of development. At salinities ranging from 21 up to 42.8, viable nauplii hatched (please see p. 200 of Barnes & Barnes 1974, for full details). Cawthorne (1978) investigated the tolerances of newly released nauplii of *Austrominius modestus* to sinusoidal, abrupt and steady changes in salinity, while Bhatnagar & Crisp (1965) investigated the time-temperature-salinity relationships for survival of the first-stage nauplii of *Austrominius modestus* (as well as *Semibalanus balanoides* and '*Chthamalus stellatus*'). At normal temperatures, salinities below 12 or above 50 caused complete immobility (Bhatnagar & Crisp 1965).

Salinity tolerance of barnacles is independent of size (Foster 1971b), and those of the adults of *Austrominius modestus* (Foster 1970) are similar to their early nauplii (Bhatnagar & Crisp 1965). The adults of *Austrominius modestus*, along with other species of acorn barnacle tested, have been found to be osmoconformers (Foster 1971b, Davenport 1976). Although adult *Austrominius modestus* are able to tolerate brackish waters, they are not as tolerant to low salinities as the estuarine barnacle *Amphibalanus improvisus* (see details subsequently). Barnacles can adjust to small changes of environmental salinity by tissue acclimation, allowing free exchange between the external medium and the mantle cavity. However, if the salinity change is too great, they can withdraw into the shell and close the mantle cavity (Foster 1971b, Davenport 1976). In aquaria, when salinity repeatedly fell to 20% seawater, Davenport (1976) found that they could survive indefinitely, and he noted that they often encounter virtually freshwater in the field. Prasada Rao (1999) pointed out that in tropical barnacles, the closure of the opercular valves at critical salinities, with the formation of a pneumostome, is a similar response to that of *Austrominius modestus* and *Balanus crenatus* from other regions. Foster (1971b) followed up his laboratory observations with field observations on the effects of salinity and desiccation on the determinants of the upper limit of the intertidal distribution of *Austrominius modestus* and *Semibalanus balanoides*. The blood concentration of both species, naturally subjected to temporary freshwater influences during tidal emersion, confirmed that the adverse effects of salinity and desiccation are avoided by closure of the opercular valves before the blood reaches intolerable dilutions. On a sheltered shore, desiccation death of both species was observed at levels in the range between spring tides (Foster 1971b).

After experimental or natural acclimation, *Austrominius modestus*, *Semibalanus balanoides* and *Balanus crenatus* are tolerant to salinities down to 14 to 17 (Foster 1970, Davenport 1976). Although intertidal *Austrominius modestus* and *Semibalanus balanoides* from the same habitat (e.g. from a shore experiencing full salinity seawater) showed similar responses to osmotic stress because of acclimation, *Austrominius modestus* may, with acclimation, be slightly more tolerant of low salinity (Foster 1970, 1971b). However, the estuarine *Amphibalanus improvisus* can, with gradual acclimation, be induced to be active at much lower salinities (~2 or even as low as 1.1) than the other three species of barnacle. This has been attributed to a wider tissue resistance by *Amphibalanus improvisus*, tolerating considerable dilution of its blood and not to any ability to regulate. This enables *Amphibalanus improvisus* to dominate where other barnacle species are excluded by prolonged periods of low salinity (Foster 1970). Davenport and other authors (1995) reported that another member of the Subfamily Elminiinae, *Elminius kingii*, is one of the few benthic invertebrate faunal species present in the Laguna San Rafael (Southern Chile). They noted that its presence there suggests that it is as tolerant to low salinity as the cosmopolitan low salinity specialist *Amphibalanus improvisus*.

Salinity affects cirral activity of barnacles, with cirral beating of *Austrominius modestus* limited to salinities above 17, while two tropical barnacle species tested continued to be active at lower salinities (Foster 1970). However, this result may have been due to the narrow annual range of salinities (32–34) experienced by *Austrominius modestus* at the site where it was collected in the Menai Straits (Foster 1970), since samples from a site where the salinity varied from ~0 at low tide to 20 at slack high water showed acclimation, with *Austrominius modestus* being active in seawater dilutions down to about 14, compared to about 21 for the Menai Straits samples. Optimum cirral beating was at a salinity of 30, while there was no activity above 53 (Foster 1970).

Shell structure

Crisp (1958) reported that the shells of *Austrominius modestus* are less resistant to mechanical damage than more open water species of barnacle. The absence of *Austrominius modestus* from wave-exposed shores has been attributed to the relative fragility of the shell (Foster 1971b, 1982), since when there was no wave action, *A. modestus* survived ~30–60 cm higher that *Semibalanus balanoides*. When the composition of barnacle shells (calcium carbonate and organic matter are the main components) was examined, organic matter constitutes <1% of the weight of the shell in *Austrominius modestus*, *Semibalanus balanoides* and various *Balanus* species, but >2% in some *Chthamalus* species (Bourget 1974, 1977, 1992). Although the two members of the Subfamily Elminiinae, *Austrominius modestus* and *Elminius kingii*, contain the same three types of shell microstructure types (granular, orientated prisms and radiating prisms), there are differences in the number of layers and also in the way that the organic matter is organised. *Austrominius modestus* has a two-layered shell, with the wall plates consisting of a simple granular arrangement of small crystals, unlike that of other Elminiinae (see details of other differences in Bourget 1977). For example, *Elminius kingii* has thick organic sheets and pillars of orientated crystals. In contrast to *Austrominius modestus*, the type of shell structure and organisation seen in *Elminius kingii* and chthamalids is believed to be very resistant to wave action (Bourget 1992).

Levels of trace elements in the shell vary with environmental factors, with an increase in Manganese in *Austrominius modestus* and *Semibalanus balanoides* being related to salinity. For both species, Manganese:Calcium and Magnesium:Calcium decreased with decreasing shore levels, while the Strontium:Calcium levels varied in the opposite direction (Bourget 1974). Bocquet-Védrine (1964, 1965) explored the relationship between the production of the epicuticle and cuticle layers, as well as that of the opercular membrane, and moulting in *Austrominius modestus* and how it differed from '*Chthamalus stellatus*'. In *Austrominius modestus*, the activity of the epidermis at the basal growth zone is discontinuous and synchronised with the moulting cycle (Bocquet-Védrine 1965). Bubel (1975) subsequently carried out an ultrastructural study of the mantle, its membrane-secreting cells and membranes in relation to shell formation. The number of calcareous growth bands laid down by *Austrominius modestus* has been seen to coincide with the number of tidal immersions (Crisp & Richardson 1975). Gollety et al. (2008) reported that the organic and $CaCO_3$ production was much higher in *Austrominius modestus* than *Chthamalus montagui*, particularly at a site which was dominated by *A. modestus*, where CO_2 fluxes were actually higher than those estimated for coral reefs, which highlights the importance of calcification in temperate marine invertebrates, such as *A. modestus*. Furthermore, at their sites at Roscoff, France, much higher $CaCO_3$ production values were obtained for the *Austrominius modestus* populations (1803.9 g_{CaCO_3} m^{-2} $year^{-1}$ and 481.0 g_{CaCO_3} m^{-2} $year^{-1}$) than those from further south in the Arcachon Basin, where the annual rate was estimated to be 1.02 g_{CaCO_3} m^{-2} $year^{-1}$ (Barnes 1971).

Size, growth rate and age

Subsequently is summarised what is known about the size, growth rate and age of *Austrominius modestus* and how they vary with latitude and various environmental parameters, including whether the individuals are intertidal or subtidal. Similar to other barnacle species, *Austrominius modestus* shows faster growth rates in early life, growing more slowly later, as it increases in size (Barnes & Barnes 1962, Anderson 1994). As an *Austrominius modestus* individual grows, it orientates itself to the water current, so that the cirral net faces the current. Growth rate varies with food availability and speed of water flow, with faster growth rates occurring subtidally and lower on the shore than higher up, and non-breeding *Austrominius modestus* grow faster than those with egg masses. Crisp & Patel (1961) noted that the growth of the opercular valves appears to be less dependent on environmental factors than other shell parts, but usually the rostro-carinal diameter (RCD) is measured. Most studies on growth rates give linear measurements, which can vary quite a lot depending on prevailing conditions, citing a factor of three for *Austrominius modestus* versus three and a half to seven for three other species mentioned (Anderson 1994).

Size in Australasia

In its native range, the smallest juvenile *Austrominius modestus* recorded had a rostro-carinal diameter of 0.5 mm, while the maximum adult RCD was 13 mm (Moore 1944). The greatest height is 9 mm (Moore 1944) to 10 mm (Jones 1990), while the average size is c. 5 × 4 mm (Moore 1944). Juvenile *Austrominius modestus* show no trace of colour, being almost transparent (Moore 1944). In New Zealand, at Queen's Wharf, Port Nicholson, Wellington, Ralph & Hurley (1952) recorded that after four weeks of deployment, the diameter of *A. modestus*, on their subtidal (1.2 m below low-tide level) Oregon pine test blocks, ranged from 1.0–2.0 mm (average 1.5 mm), where the smallest individuals were found on vertical and silted areas. At Lyttleton, South Island, NZ, on subtidal panels that had been deployed for one month, the maximum RCD reached was 2.6 mm, but Skerman (1958) pointed out that they may not necessarily have been one month old (due to a lag in settlement), so they may attain larger sizes in a month. After six months on these panels, the maximum size attained by *Austrominius modestus* was 6.5 mm RCD. On the panels that had been deployed by Ralph & Hurley (1952) for 13 months, the maximum size was 6.0 mm, but the age of these was unknown.

Size in Europe

More research has been published on size and rates of growth of *Austrominius modestus* in its invasive than native range. Average RCD is similar to its native range, but a larger adult shell size (maximum RCD of 17 mm) has been recorded under certain environmental conditions in Europe (see subsequently). Tighe-Ford et al. (1970) found that the growth rates of recently settled *Austrominius modestus* in the laboratory were greater in flowing seawater in comparison to static seawater, despite the water being changed and food added in the latter situation. *Austrominius modestus* can show rapid growth when there is plenty of food available (Southward 2008), but usually has a slower growth rate than *Semibalanus balanoides* (Crisp 1964a). Crisp (1964a) gave a dry tissue weight increment of body (excluding shell) of 0.16–0.25 mg dry wt body d^{-1} (0.12–0.18 d^{-1}) (at 13–17°C). Rainbow & Wang (2001) pointed out that this is much higher than that measured in other species of barnacle, so, in their modelling of metal accumulation (see subsequently), they used much lower growth rate constants (0.002–0.01 d^{-1}), which had been determined in other barnacle species. In laboratory conditions, 15 weeks after settling, *Austrominius modestus* could measure 6 to 8 mm (Tighe-Ford et al. 1970), which is in the 'normal' size range (5–10 mm) of adult *A. modestus* suggested by Southward & Crisp (1963). Gollety et al. (2008) have carried out some of the most detailed work comparing the growth rates of intertidal *Austrominius modestus* and *C. montagui* at Roscoff, France, over a 13-month period, including calculating yearly size:weight allometric relationships and following the growth rates of different cohorts. *Austrominius modestus* showed a steadier growth than *Chthamalus montagui*, and the largest *C. montagui* reached 7.9 mm, in comparison to 9.4 mm for *A. modestus* (Golléty et al. 2008), comparable to the maximum size of 9.8 mm observed for subtidal *A. modestus* at Helgoland (Anger 1978). In The Netherlands, intertidal specimens could reach a maximum of between 6 and 8 mm in their first year and 11 and 12 mm in their second year, although one individual measured 12.2 mm (Hartog 1953).

Stubbings (1950) reported that subtidal specimens may reach a maximum of 4–5 mm in RCD at four weeks old in June–July, but in Helgoland, Germany, they reached only 3 mm after a month of settling, attaining 9.8 mm after one season (when water temperatures were 13–16°C, with the largest measured being 10.4 mm) (Anger 1978). Individuals at the edges of subtidal plates showed greater growth than those in the centre (Crisp & Davies 1955). Anger (1978) noted that the growth rates that he recorded were similar to those of Kühl (1954, 1963) for the German Bight area.

Growth and environmental conditions

Barnes & Barnes (1962) mentioned that, although *Austrominius modestus* is eurythermal, moderately high temperatures (e.g. 15–20°C) favour growth. The growth rate of *Austrominius modestus* was examined towards the northern part of its introduced range in Scotland, at Stranraer and Kirkcolm, where the annual temperature range was 4–16°C, and Millport, Isle of Cumbrae, in the Firth of Clyde, where winter temperatures were slightly higher, but maximum summer temperatures are lower than 16°C (Barnes & Barnes 1962). When growth was compared at different intertidal heights and subtidally (on a raft) and in muddy versus relatively open water conditions, growth took place at a fairly uniform rate in summer and autumn following settlement, but there was little growth in winter. Barnes & Barnes (1962) reported faster growth rates subtidally and lower on the shores; that is, *Austrominius modestus* that had settled in August had, by late autumn, reached a RCD of 8.6 mm on the raft and 6 mm at low tide level, but only 5 mm at the upper level (~2.7 m higher). The average size of adult specimens was 5–6 mm in Chichester harbour (Stubbings 1950) and was similar to that recorded for the species in Australia (Pope 1945) and New Zealand (Moore 1944), and in summer this size is reached in about two months. However, Bishop (1947) reported that, in June and July, in just 40 days, subtidal specimens in Chichester harbour could reach 6 mm, but grew less rapidly than *Amphibalanus improvisus*. However, Stubbings (1950) noted that the maximum size (9 mm) recorded in Chichester harbour was well below the 12.5–13.0 mm recorded in Australasia. He attributed the failure to reach the upper limit of size to the lower average surface water temperatures there, in all seasons, in comparison to their original habitat.

Growth rate was found to increase with access to previously unfiltered water and rapidly moving water, with individuals in fast-flowing water growing rapidly to reach a large size (10–15 mm) (Crisp & Davies 1955), which is larger than recorded in their native habitat. Even larger specimens were reported by Bishop (1954). These measured up to 17 mm and were found in Northern Finisterre, France, in narrow drowned river valleys, where there are large tidal ranges, which produce very fast currents. He suggested that this large size could be attained due to these very favourable environmental conditions, rather than age. Crisp & Patel (1961) discuss the potential reasons for growth rate slowing down after a certain size/maturity.

In south-west Ireland, *Austrominius modestus* recruits ultimately attained a larger opercular diameter than recruits of both native species, *Semibalanus balanoides* and *Chthamalus montagui* (Gallagher et al., unpublished data) (see Figure 2). The native species *Semibalanus balanoides* was found to display rapid growth in the first few months following settlement, allowing it to rapidly utilise space prior to the peak of *Austrominius modestus* settlement. This fast initial growth rate (see Plate 2) may provide the native species with a competitive advantage over *A. modestus,* allowing both species to persist in some locations. Plate 2 shows fast initial growth of *Semibalanus balanoides* and subsequent good survival of *S. balanoides*, in particular those that attained a large size initially. Continual settlement of *Austrominius modestus* can be observed, as can relatively high levels of adult mortality.

Crowding and growth: Anderson (1994) pointed out that crowding affects growth patterns (see 'Reproduction' subsequently also). He noted that the response to crowding of low-growing species, such as *Austrominius modestus*, is to grow over one another rather than becoming columnar, which is seen, for example, in *Chthamalus stellatus.*

Growth rates of breeding and non-breeding Austrominius modestus: Growth rates of *Austrominius modestus* vary depending on whether they are breeding. Crisp & Patel (1961) examined growth rates with age (from settlement to over 200 days, in summer to autumn) of 0+ non-breeding and breeding of *A. modestus* on panels continuously immersed in the Menai Straits, Wales. For both groups, growth was approximately linear with respect to time, until they reached 5–7 mm in RCD. Subsequently, those that could not breed (being isolated by >5 cm) then grew significantly faster and to a larger size than those that were able to cross-fertilise and breed, which they concluded

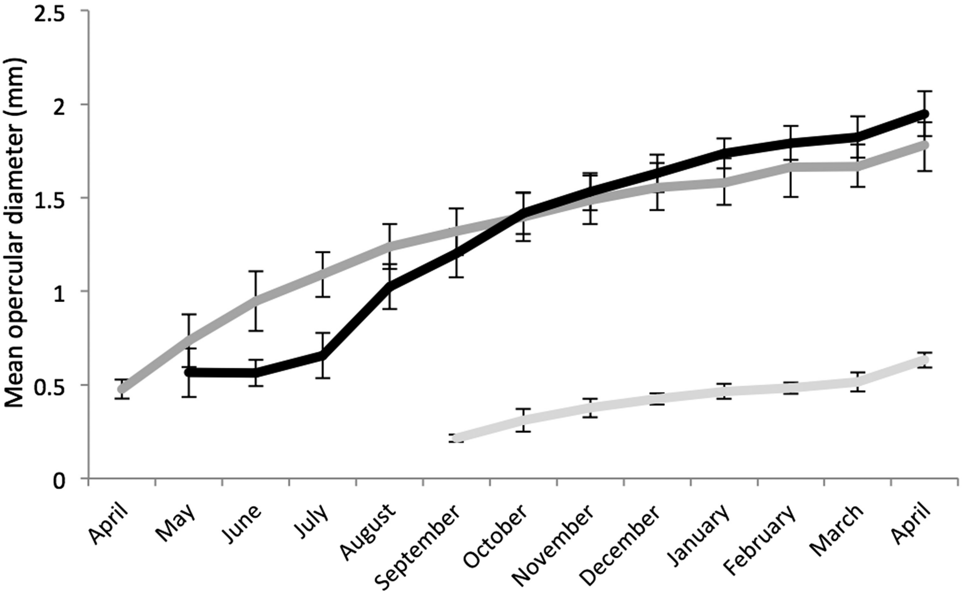

Figure 2 Mean (±SE) opercular diameter (mm) of *Semibalanus balanoides* (dark grey), *Austrominius modestus* (black) and *Chthamalus montagui* (light grey) at monthly intervals from April 2014–April 2015. Mean values were calculated from recruits in removal plots across six sites ($n = 108$ plots) in south-west Ireland.

was due to the loss of tissue in the form of eggs. After six months, the non-breeding individuals were ∼10% larger in linear dimensions (except operculum) (see Table 8, p. 113 of Crisp & Patel 1961, for details), with a 30% greater volume and a total weight of 40% greater. Crisp & Maclean (1990) calculated the wet weight and volume index (L × B × H) of *Austrominius modestus* and found that it was closely correlated. Growth rates of these non-breeding and breeding *Austrominius modestus* on subtidal panels also varied when in potential competition with their own species or with *Semibalanus balanoides* (Crisp & Patel 1961). Although *Semibalanus balanoides* may be four times heavier than *Austrominius modestus*, growth of non-breeding individuals of *A. modestus* remained greater than breeding ones, confirming that the loss in weight previously was due to reproduction rather than competition for food.

Longevity: *Austrominius modestus* is likely short lived (Knight-Jones & Stevenson 1950) with a lifespan of just two to three years. Harms & Anger (1983) suggested less than two years, while Gollèty et al. (2008) proposed at least 22–24 months, depending on the month in which recruitment

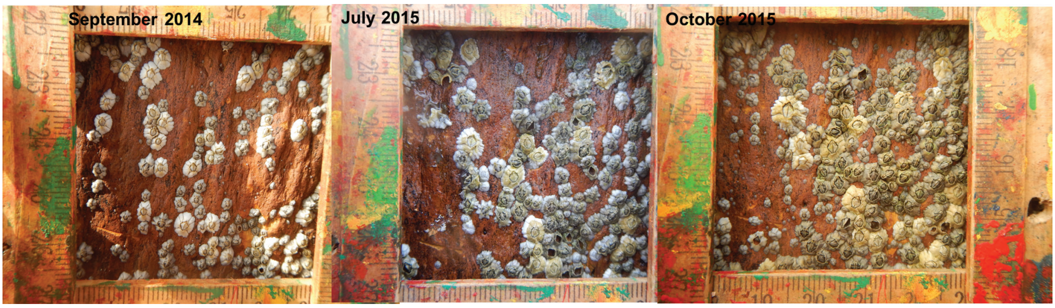

Plate 2 Photos showing growth and survival of *A. modestus* and *S. balanoides* over a 13-month period in removal plots at Ballyrisode, Co. Cork, Ireland, by M.C. Gallagher.

occurred. Crisp & Davies (1955) followed individuals on subtidal panels for 21 months, but this was under experimental conditions where new settlement was removed. Foster (1971b) noted that the highest specimens of *Austrominius modestus* on many shores are large specimens for this species, perhaps indicating that once they become established, they may live for long periods, but he did not suggest for how long they may live.

Growth in silty/muddy conditions: Crisp (1958) had suggested that since *Austrominius modestus* is euryhaline and often most abundant in muddy estuaries, they may be specially adapted to feed on detritus. However, Barnes & Barnes (1962) found that at moderately low temperatures, growth was equally good in muddy and open water areas. They suggested that this may indicate that they could use detritus and open coastal plankton equally well. Moore (1944) noted that 'Darwin picked on the most striking ecological attribute of *E. modestus*, its ability to withstand brackish and very muddy water'. Anon (1948) suggested that in its introduced range, it seemed to be able to withstand muddy waters in estuaries better than some native barnacle species. By 1979, *Chthamalus montagui* had disappeared from Mont St Michel, France, being replaced by *Austrominius modestus*, which was attributed to *A. modestus* being better adapted to the rapid silting-up of this part of the Bay of St. Malo (Crisp et al. 1981). One reason, along with its tolerance of low salinity, *Austrominius modestus* can survive in estuarine conditions is that its tough cirri can cope with the turbid conditions. Crisp & Davies (1955) noted that the fact that it can breed at a wide range of temperatures (see subsequently) makes it well suited to living in shallow estuaries and sheltered coasts in temperate latitudes.

Shell orientation: Although at settlement, orientation to the water current is negligible, as it grows, *Austrominius modestus* orientates itself to the water current, so that the carina points away usually from the current source, meaning that the cirral net faces the current (Crisp & Stubbings 1957). Most of the *Austrominius modestus* and *Balanus crenatus* on subtidal plates were orientated with their carinae at an acute angle to the water surface (Anger 1978). This orientation was due to light (Anger 1978) and the predominant sea surface current direction (Crisp & Barnes 1954, Crisp & Stubbings 1957). Barnes et al. (1951) found no observable change in orientation during growth in *Austrominius modestus*.

Endocrinology

The small amount of research to date on the endocrinology of *Austrominius modestus* has focused on the processes and substances controlling hatching, larval metamorphosis and moulting. Clare (1987) pointed out that some of the most detailed work on cirripede endocrinology concerns the histology of the neurosecretory centre and the processes that control moulting and egg hatching. McGregory (1967) examined the central nervous system for the presence of neurosecretory granules of a number of acorn barnacle species, including *Austrominius modestus*. He found that the neurosecretory granules, stained with paraldehyde fuchsin (PF), measured about 0.2 μm in diameter. Control of moulting involves ecdysteroids and a moult-inhibiting hormone. Clare (1987) mentioned that one of the first indications that ecdysteroids were present in barnacles was when unpublished research by D.B. Carlisle showed that extracts of adult *Austrominius modestus*, injected into Y-oran-ablated *Carcinus maenas*, induced the crabs to moult. Tighe-Forde (1977) found that two analogues of insect juvenile hormones (JHs) interfered with the development of *Austrominius modestus* larvae, suggesting that a JH or analogue controls larval moulting. When stage VI nauplii metamorphosed into cyprids, they were morphologically abnormal, retaining some naupliar characteristics, and were significantly smaller in size than usual (see Table I of Tighe-Forde 1977). When he then examined the effect of the two analogues on the metamorphosis of the cyprids, he found that many of the farnesyl methyl esther-treated cyprids were morphologically abnormal. The Ro-8-4314-treated cyprids did not show these abnormalities, but were in general larger than the control ones and in comparison to the control, significantly more of those that had metamorphosed into young adults were unattached.

Tighe-Forde (1977) suggested that these effects may be related to the physiological development of the larvae at the time of exposure. Mortlock et al. (1984) also reported abnormalities, but different to those found by Tighe-Forde (1977), when they exposed *Austrominius modestus* nauplii to another JH analogue, ZR 512. Metamorphosis of nauplii to cyprids and then to adults was accelerated at farnesol concentrations of 1 ppm. The hatching substance produced by the barnacle's own metabolism has been identified in *Austrominius modestus* and is covered in the 'Reproduction' section subsequently, along with the delay of ecdysis during brooding of the embryos.

Excretion

White (1992) and Anderson (1994) summarised what is known about excretion in barnacles, including the organs responsible and the main nitrogenous wastes. Most is known for *Semibalanus balanoides*, but White (1992) mentions Bubel's (1975) research on *Austrominius modestus*. In contrast to other mantle regions, the inner mantle hypodermis was found to show specialisations which were characteristic of a transportive epithelium, suggesting that they could function as a site of nitrogen release (Bubel 1975). The antennal glands are the excretory organs in the nauplii, and Walker (1973) described the frontal horns and associated gland cells of the nauplii of *Austrominius modestus*, *Chirona hameri* and *Semibalanus balanoides*.

Reproduction

Fertilisation

Austrominius modestus is an obligatory cross-fertilising hermaphrodite (Crisp 1950, Barnes & Crisp 1956), needing to be within a maximum of ~5 cm (i.e. the maximum extension of the penis, Barnes & Crisp 1956, Crisp 1958) from another individual to reproduce, unlike some other species of acorn barnacle which may self-fertilise in certain situations (see examples in e.g. Barnes & Crisp 1956, Barnes 1992). Flowerdew (1984) confirmed this obligatory cross-fertilisation when he found no evidence of inbreeding at up to nine loci. Similar to many other thoracican cirripede species, *Austrominius modestus* has a diploid count of 32 chromosomes, and the size of its nuclei and chromosomes at prometaphase (9.2 μm and 1.4–2.7 μm, respectively) are in the middle of the range of those species studied (Austin et al. 1958).

The mating group size of *Austrominius modestus* is generally four to seven, that is, mating involves up to seven 'males' donating sperm to a 'female', which is in line with it being a small barnacle in size, since they have the largest mating groups (Charnov 1987 citing Crisp as a pers. comm.). Foster & Nott (1969) described the sensory structures in the operculum of *Austrominius modestus* and how a functional female remains open when contacted by a penis, allowing penetration.

Age and size at breeding

In barnacles, sexual maturity is mainly a function of size but is also, to a limited degree, dependent on age (Crisp & Patel 1961). *Austrominius modestus* has been described as fast maturing and being able to breed at a very young age (Luckens 1975). Within its native range, in Ngataringa Bay, Auckland Harbour, New Zealand, Moore (1944) reported that they reached maturity and released larvae within two and a half to three months of settling. In its introduced range, reproduction can begin at an even younger age, with some fast-growing specimens in Great Britain containing embryos within as little as six to seven weeks of settlement (Crisp & Patel 1961) at a RCD as small as 3 mm, if continuously submerged, thus reaching maturity at a smaller size than *Semibalanus balanoides* (Crisp 1964b). Half of a studied population contained fertilised egg masses within 10 weeks of settlement and all by 12 weeks (Crisp & Patel 1961). Crisp & Davies (1955) noted that, by then, these young individuals had reached a breeding equilibrium, which was indistinguishable from older populations, unless the older barnacles were infected by the parasite *Hemioniscus balani* Buchholz (see subsequently). Stubbings (1950), as cited by Southward (2008), commented that during the summer, *Austrominius modestus* may reach maturity within eight weeks of settlement, which has also been seen in some individuals in Helgoland, Germany (Harms & Anger 1983). In Helgoland Harbour, some 0+ individuals on subtidal plates which had reached 3 mm in RCD were large enough to reproduce (Anger 1978), similar to that found by Crisp & Davies (1955) in Great Britain for a few of their continuously submerged specimens, most of which measured 4–6 mm in RCD. A similar young age of first reproduction has been seen in *Chthamalus anisopoma* and *Chthamalus fissus*, in California, at an age of ~six (Malusa 1986) and eight (Hines 1978) weeks, respectively, as well as some *Balanus* species (see references within Barnes 1989).

Terminology associated with the reproductive cycle

Crisp & Davies (1955) defined the various terms associated with the reproductive cycle of a single brood of *Austrominius modestus*. The brood period (T) is the time from one fertilisation (oviposition) to the next and consists of the fertilised period (T_F) (from oviposition to release of nauplii, i.e., the length of embryonic development) and the empty period (T_E) (from release of the nauplii to the next fertilisation and oviposition), while early embryonic development (T_D) is normally shorter than the fertilised period. See Crisp & Davies (1955) for the definition of other terms and how to calculate the fraction of the population with embryos and so on. In this paper, the definitions of egg and embryo follow Barnes (1989) from her review of egg production in cirripedes. The term egg refers to the fertilised ovum, from which in *Austrominius modestus* the stage I nauplius hatches. The term embryo refers to the young organism developing within the egg or embryonic capsule. Walker (1992) provides a good overview of the reproduction of barnacles in general, including the structure of the gonads.

Development of the gonads

The gonads of individuals in a population of *Austrominius modestus* are not necessarily synchronous (Crisp & Davies 1955), which is very different to *Semibalanus balanoides* and *Balanus balanus,* in which the gonads are in a uniform state at any given time. In the laboratory, Patel & Crisp (1960b) were able to induce a range of barnacle species to develop gonads within two to three weeks when fed and kept at an appropriate temperature. For *Austrominius modestus*, the lowest critical breeding temperature at which fertilised embryos were found was 8–9°C. Barnes (1989) noted the importance of temperature since it sets limits to reproduction, thus becoming ecologically important in the latitudinal distribution of cirripedes, but she warned that it can be difficult to distinguish the effect of temperature from latitude.

Subsequently we have summarised what is known about the development of the male and female gonads of *Austrominius modestus*, including the length of breeding season, the level of brooding (usually presented as %), the number of broods per year and what is known about how they vary in their native and introduced range with environmental parameters. However, much less has been published about any variation in the cycles of this species, especially regarding the development of the male gonads and ovary, than, for example, *Semibalanus balanoides*. There is plenty of scope for further targeted research, which would be particularly pertinent at the current known northern and southern limits of its introduced range. Barnes (1989) had noted that warm-water species with their northern limits of distribution in Europe may have more than one breeding cycle during warmer months but will have more cycles further south. The fact that reproduction can occur over a wide range of temperatures allows *Austrominius modestus* to thrive in sheltered coasts as well as in estuaries in its introduced range, where there can be wide fluctuations in temperature but an abundant food supply throughout most of the year (Crisp & Davies 1955). Although it is eurythermal, moderately high temperatures (e.g. 15–20°C) favour breeding (Barnes & Barnes 1962), as well as growth, as previously mentioned.

Crisp (1954) described the male and female reproductive organs of *Balanus balanus* (formerly *Balanus porcatus*) and provided scoring systems to stage the development of the testis tissue, vesiculae seminales and ovary, which have been adapted and modified for use in staging the gonad development of *Austrominius modestus* (see O'Riordan & Murphy 2000).

The male reproductive system

Austrominius modestus has been described as slightly protandrous due to the fact that male gonads can be found at smaller body sizes than the ovaries. In Great Britain, male gonads developed in *Austrominius modestus* at a RCD of 3 to 5 mm, with the testes and vesiculae seminales reaching full development in animals greater than 5 mm (Crisp & Patel 1961). Minimum size of first breeding has not been examined in Ireland yet. In Great Britain, those with a RCD of 5 mm or greater always had male gonads throughout the summer months. The same authors observed that crowded intertidal *Austrominius modestus* eventually developed male gonads at a smaller size and had longer penes than normal uncrowded subtidal *A. modestus* of the same size.

As far as the authors are aware, O'Riordan & Murphy (2000) is the only published paper examining the state of the testes and vesiculae seminales throughout the year, for either its introduced or native range. They compared the reproduction of *Austrominius modestus* over a 15-month period at three sites within a small bay in southern Ireland (51°50′N, 08°14′W): site one was adjacent to a the outlet pipe ('outfall') of a power-generating station, site two was toward the eastern part of the bay, while site three was where a freshwater stream (salinity of 0.1 to 0.6) ran into the southern part of the bay and where the lowest air and seawater temperatures were recorded. At site one, the salinity at low tide in the remaining water varied from 26.3–47.8 and air and water temperature were slightly higher than at the other two sites. The discharged seawater, which had been used for cooling the system, was 9–10°C above ambient. The testes and vesiculae seminales of *Austrominius modestus* showed an annual cycle of development, with the highest percentage with well-developed stages occurring in late summer, but moderately developed stages could be found in all months sampled at all three sites. In most months, a higher percentage of animals had well-developed testes than vesiculae seminales. The male gonads were least developed from October–December, most likely due to lack of food, after which they began to regenerate. The proportion of animals with well-developed testes was four times less at its peak at the outfall site than at the other two sites, and they only occurred in seven months. Each month, many of the barnacles at the outfall site lacked testes and vesiculae seminales, or the testes were poorly developed and vesiculae seminales were thin linear sacs with little sperm. Murray (2009) examined the state of the male gonads during a three-month period in summer 2009, at Lough Hyne Marine Nature Reserve, Cork, south-west Ireland. A higher proportion had moderately to well-developed testes and vesiculae seminales in late summer (August) than in early summer (June or July) (Murray 2009). For specimens collected in June from LWN near Plymouth, Great Britain, copulation in the laboratory occurred between 4 and 15°C (Southward 1955a). In south-west England, submerged specimens had somewhat reduced male organs in the late autumn and winter, but they were still present. Thus, reduced levels of brooding at this time of year may be due to lack of food for the re-development of the ovary (Crisp & Davies 1955). In comparison to the reserves needed for the ovary and egg masses, the loss of seminal fluid has been suggested to be either a negligible drain on resources or a common factor in both breeding and non-breeding specimens (Crisp & Patel 1961). However, Barnes (1992) noted that for samples taken in Arcachon Bay in France, the loss of semen results in a significant loss of body weight when the seminal vesicles are full.

Penis structure, extension and ecdysis: The penis of *Austrominius modestus* is minutely annulated, with a circlet of small setae distally, but it does not have a basidorsal point (see Figure 25K of Jones 1990). The penis of *Austrominius modestus* thus differs from balanids, in lacking this basidorsal point (Foster 1978). In Great Britain, Crisp & Patel (1961) measured the length of the penis with respect to the RCD, finding that in *Austrominius modestus* the penis was absent in very small animals, but it developed heterogonically in specimens of 3–5 mm diameter, thereafter growing more slowly. The penis of *Austrominius modestus* is much longer than its cirri, emerging between cirri I and II (Moore 1944), and fast beat cirral activity precedes the extension of the penis (Anderson 1994).

Within the Balanomorpha, the regression and/or loss of the penis seems to depend on how frequently the animals breed within a season and that the number of penis annulations follows the breeding season (Barnes 1992). In *Semibalanus balanoides*, which just produces a single brood per year, the first moulting after a period of anecdysis contains all of the tissues of the penis, and a new penis then gradually develops (Crisp & Patel 1958). However, Barnes (1992) found that in *Austrominius modestus* from Arcachon Bay, France, none were lacking a penis, but there was a greater percentage with penes with fewer annulations in March (40%), August (30%) and October (10%), and these penes had the appearance of regeneration rather than degeneration. However, she warned that the degeneration phase might have been missed due to the sampling regime. The maximum number of penis annulations recorded by Barnes (1992) for *Austrominius modestus* was 240. Further north, in southern Ireland, although they did not measure the number of penis annulations, a penis was present throughout the year in all of the more than 2000 specimens of *Austrominius modestus* examined over a 15-month period (O'Riordan & Murphy 2000). However, in summer 2009, and summer 2019, at Lough Hyne Marine Nature Reserve, Cork, Ireland, up to 20% and 24% respectively of samples lacked a penis (Murray, 2009; Swain, 2019). In winter 2019–20, a penis could not be found in between 2 and 39% of *Austrominius modestus* samples collected on shores in Cork (O'Sullivan 2020).

The spermatozoa of barnacles, unlike most other crustaceans, are flagellated and are usually immobile in the seminal fluid (Barnes & Crisp 1956), but the spermatozoa of *Austrominius modestus* (and *Semibalanus balanoides*) become extremely active either after being discharged through the penis into the mantle cavity of another individual or when treated with chelating agents, such as ethylene diamine tetra-acetic acid (Crisp, unpublished observation; cf. Fujii et al. 1955). Barnes et al. (1971) examined the spermatozoa and spermatogenesis of various cirripede species, including *Austrominius modestus*, while Klepal (1990) described both the spermatozoon and accessory droplets. The sperm ultrastructure and its phylogenetic significance have been described for 46 species of cirripedia, including a number of members of the Subfamily Elminiinae, but not *Austrominius modestus* (Healy & Anderson 1990). An accessory droplet is usually present in thoracican barnacles, with that of *Austrominius modestus* being represented by a thickening (Barnes et al. 1971). In April (1970), in Arcachon, France, all of the vesicular spermatozoa examined had either a very narrow non-refringent droplet (thickening) or were fully filiform, with only slight motility (Barnes et al. 1971).

The female reproductive system

The ovary and ovarian regeneration

Size of ova and ovarian development

In comparison to many other barnacle species (see Table III of Crisp 1954, and Table XV of Barnes 1992), the ova of *Austrominius modestus* are relatively small (see Table 1), ranging from 20–40 μm in the earliest stages up to 100–150 μm for a fully developed ovum (Crisp & Patel 1961) or a mean diameter of 125 μm (Crisp 1954). Although there are little published data on ova size in cirripedes, ovum size (volume) is known to be determined within very strict limits (see Crisp 1986 1987, Walker 1992). When reproductive energy is low (e.g. due to lack of food), it is the number of ova that is

Table 1 Size range of ova *A. modestus* when embryos were in different stages of development, adapted from Crisp & Patel (1961)

Size range of ova (μm)	Stages of development of embryos (see Crisp 1954)
20–40	1–4
30–60	5–7
40–100	8–10
70–120	11–12
80–120	13
100–150	Nauplii liberated

reduced, rather than their size (Patel & Crisp 1960b) and biochemical composition (Walker 1992). Barnes & Barnes (1965a,b) had noted that there is a marked effect of adult barnacle size on the size of ova and embryos.

The stage of development of the ovary can be determined by its colour and texture, and Crisp & Davies (1955) used a numbering system to describe the development of *Austrominius modestus*'s ovary, which followed Crisp's (1954) research on *Balanus balanus*. This and one used by Burrows (1988) for *Chthamalus* were later adapted and modified by O'Riordan & Murphy (2000) for *Austrominius modestus* (see their Table 1). However, with respect to the colour, Patel & Crisp (1960b) cautioned that if adult *Austrominius modestus* in the laboratory are fed with *Artemia* larvae, the colour of the newly developed ovary shows a pinkish tinge, instead of the normal yellow.

Samples of *Austrominius modestus* from southern Great Britain contained only a few individuals of ~3 mm RCD with any sign of ovarian development; embryos were rarely present in individuals less than 4 mm, with ovarian maturity occurring at ~6 mm (~40 days) (Crisp & Patel 1961), while, as mentioned previously, male gonads could be present from 3 mm. In southern Ireland, O'Riordan & Murphy (2000) found that, similar to the male gonads, the ovary of intertidal *Austrominius modestus* (all >4 mm RCD) showed seasonal changes, with the highest percentage with well-developed ovaries in the summer. Although less well-developed stages could be found throughout the year, it was in the winter months that the maximum proportion lacked any sign of ovaries. Similarly, in south-west England, Crisp & Davies (1955) noted that, for continuously submerged specimens on glass plates suspended 1.8 m below sea surface, the ovaries were small and poorly developed in late autumn and winter, but by the time the individual was fertilised, the ovarian tubules were nearly completely full of mature eggs. In April (1970), in Arcachon, France, most of the population had well-developed ovaries, with a small number with developing ovaries at a time when 23%–27% had embryo masses (Barnes et al. 1971). At Lough Hyne Marine Nature Reserve, Cork, Ireland, in summer 2009, the percentage with no ovary visible increased from June (13.4%), through July to August (63.4%). However, the percentage brooding embryos increased from June to August, suggesting that in June a batch of ova were fertilised, which developed as embryos in July and August, while another batch of ova were developing (Murray 2009).

Ovarian regeneration and the effects of food and temperature

If sufficient food is present, *Austrominius modestus* can breed continuously, with little or no interruption, with the immature ova developing as soon as nauplii are released from the embryo masses. The time taken to incubate the fertilised eggs determines the reproductive rate (Crisp & Patel 1961). Crisp & Patel (1961) showed that the smallest ova only occurred in *Austrominius modestus* that had early stages of fertilised eggs, while those which had the later stages had larger ova (see Table 1). *Austrominius modestus* eggs may be mature and ready to be fertilised as soon as the stage I nauplii are released, as seen in subtidal specimens in the Menai Straits, Wales (Crisp & Patel 1961), and intertidal populations in southern Ireland (O'Riordan & Murphy 2000). When food is present, the high reproductive rate is facilitated by the fast cirral beat of *Austrominius modestus*. However, further south, in south-west Britain, in submerged specimens in late autumn and winter, reduced levels of brooding were due to lack of food for the regeneration of the ovary (Crisp & Davies 1955). So in *Austrominius modestus*, fertilisation can occur at any time of year, as long as the ovaries have regenerated.

Reproduction can occur over a wide range of temperatures (6–20°C) in the wild, and reproduction may occur at even higher temperatures (Crisp & Davies 1955), but 15–20°C favours breeding. *Austrominius modestus* needs a sufficiently high temperature at the time of fertilisation, egg-laying and spawning, with 6.0–6.5°C being the critical temperature for the latter. In temperate areas of its invasive range, the gonads (testes, vesiculae seminales and ovary) show an annual cycle of development, with higher proportions with more well-developed gonads during summer months, but the gonads of individuals in a population are not necessarily synchronous.

Temperature affects the regeneration of the ovary. Crisp & Davies (1955) examined reproduction in continuously submerged specimens on glass plates suspended ~1.8 m below sea surface in south-west Britain, where temperatures increase in spring and early summer (range 5–18°C). They found that the ovary regenerated quickly, so that shortly after the nauplii were released, another set of eggs were fertilised to produce a new brood (Crisp & Davies 1955). However, in autumn and winter, the ovary may not regenerate for a long period of time, so a high proportion of the population will not contain embryo masses. They suggested that the fecundity of *Austrominius modestus* in south-west Britain is limited by the rate of development of the embryos in spring and summer but by nutrition in autumn and winter. Since they found that embryos were retained for a shorter time in spring and summer than in autumn and winter, they suggested that a rapidly maturing ovary at that time of year might stimulate naupliar release, but nauplii could still be released without ovarian regeneration. At similar temperatures, embryos will be released more quickly in spring than in autumn, because the barnacles are more well nourished, since more suspended food is available (Patel & Crisp 1960a).

Brood period (T) has been estimated to be as short as 14 days in the subtidal in the summer but longer in the intertidal and winter (up to 60–80 days) (Crisp & Davies 1955). During summer in the subtidal, the average brood period of 14 days was followed by hatching lasting ~10 days. But in winter, both brood and hatching periods were much longer (e.g. 60–80 days for the fertilised period T_F) and fluctuated more, even though normal development appears to occur at a wide range of temperatures. As long as enough food was available, they suggested that *Austrominius modestus* can breed down to a temperature of 6°C. Below temperatures of 6°C, embryonic development can continue, but at a very slow rate (Crisp & Davies 1955). Patel & Crisp (1960a) examined the rate of development of embryo masses, incubated outside the parent, of seven species of barnacles, at temperatures ranging from 3 to 32°C. The embryo masses of southern, intertidal and estuarine species displayed a wider range of temperature tolerance than northern, sublittoral and open coast species. *Austrominius modestus* showed embryo development at the widest range of temperature *in vitro*, from 3 to 32°C. However those at 3°C took over 50 days to develop (and were attacked by fungus) and were only liberated after the addition of a hatching substance. Development did not seem to be affected by brief periods near the freezing point. Those embryos which were removed from adults in the early stages of development failed to develop at 32°C, suggesting a greater sensitivity at these stages, since later-staged ones were able to complete development. The maximum rate of development occurred between 23 and 25°C, which they linked to the mean monthly seawater temperature (14–19°C) at the southern part of its introduced range (S. Portugal). They suggested that these relatively high temperatures may allow it to breed all year round in temperate waters, but this is currently not known and an area for further research. Patel & Crisp (1960b) slightly widened the optimum rate to 22–25°C, with 93% of the laboratory samples containing fertilised embryos at 25°C, versus only 54% and 35% at 9°C and 30°C, respectively. Barnes & Barnes (1962) commented that it takes 40 days for a brood to develop at 8–9°C, but that they occasionally found egg masses present in winter at their sites in Western Scotland.

Brooding of egg masses

Austrominius modestus may brood embryos throughout the year in both its native and introduced range, but this varies with location and latitude and maybe also salinity (see O'Riordan & Murphy 2000). Subsequently we describe how the length of brooding season, the level of brooding, the number of broods per year and fecundity vary with location and some key environmental parameters. Please see O'Riordan & Murphy (2000) for the scale for scoring the stage of development of the egg masses of *Austrominius modestus*. As they develop, the fertilised eggs, which are usually held in a pair of egg masses (see Plate 3, but see subsequently), change from white or a pale cream to yellow, grey, ochre, fawn brown.

When eggs have reached Stage 4 (and the egg masses are dark brown and kidney shaped), the eggs may be retained for quite a long time before release, although they can hatch immediately in the laboratory if removed from the parent.

Walker (1992) describes how a 'hatching substance' released by the adult barnacle causes the stage I nauplii to hatch from their embryo cases. Crisp et al. (1991) noted that although a hatching substance may not be essential in all barnacles, it is thought to be so in *Austrominius modestus* and *Semibalanus balanoides*. That used by *Austrominius modestus* is monohydroxyeicosapentaenoic acid (Hill et al. 1988) and is released by the adult into the mantle cavity, usually when the adult is well nourished but not when it is starved. Decayed remains of unhatched broods have been repeatedly found beneath a new brood in *Austrominius modestus* and *Semibalanus balanoides*, implying that sufficient hatching substance was not present (Crisp et al. 1991). They summarised (Table I therein, p. 64) the evidence for delayed and spontaneous hatching of mature eggs in nine species of barnacle, including some unpublished/pers. comm. data for *Austrominius modestus* and other species. Cawthorne & Davenport (1980) found that hatching only occurred at salinities above 21 with reduced salinities, causing the adults to retain the larvae, while fluctuations in temperature induced larval release in *Austrominius modestus* but not in *Semibalanus balanoides*. According to Crisp & Davies (1955) in *Austrominius modestus*, *Amphibalanus improvisus*, *A. amphitrite* and *Balanus crenatus*, all of which can produce more than one brood per year, oviposition never occurs until the previous brood is released; thus, never more than one brood of embryos can be found. However, O'Riordan & Murphy (2000) did find a single individual of *Austrominius modestus* (out of over 2000 examined) with two pairs of embryo masses in different stages of development (stages 3 and 4),

Plate 3 *A. modestus* removed from the substrate, showing a pair of kidney-shaped embryo masses, photo taken by M.C. Gallagher.

which showed no signs of decay. This is similar to '*Chthamalus stellatus*' (probably *Chthamalus montagui* since found high on the shore), where a few individuals out of several thousand had two sets of embryo masses (Crisp & Davies 1955). Three egg masses, instead of a pair, have been seen in one (out of 437) *Chthamalus stellatus*, while a single egg mass, instead of a pair, has been recorded in both *Chthamalus montagui* (2/234) and *Chthamalus stellatus* (4/437) (O'Riordan 1992, O'Riordan et al. 1995).

Brooding season in the native range: The brooding season of *Austrominius modestus* in Australasia has been described by a number of authors (e.g. Moore 1944, Powell 1947, Wisely & Blick 1964, Foster 1967a,b, Luckens 1970, 1975, 1976). In Auckland Province, New Zealand, Moore (1944) noted that stage I nauplii have been recorded in the mantle cavities throughout the year, and it was suggested that this may be the same all around the coast. Working at Leigh, Luckens (1975) described *Austrominius modestus* as a continuously breeding species. However, Barnes (1989) commented that, in New Zealand, within the optimum temperature range and in relatively stable conditions, there is some evidence of seasonal breeding periods superimposed on a general continuous low level of reproduction. This certainly seems to be the case for some other populations at Leigh, New Zealand (Foster 1967b), with peaks in the percentage brooding in February–March and August–October. However, no embryos were recorded in either year for the November samples (see Figure 3, p. 38 of Foster 1967b), but both immature and mature embryos were found in all months when brooding was present. Zauke et al. (1992) reported that for samples collected in May 1984, 100% of the *Austrominius modestus* samples attached to mangroves in Omaha Beach contained egg masses. From their 17 sites, further south in Auckland, the percentage brooding varied from 1% to 70%. At Omaha Beach, there was a slight positive correlation ($r = 0.478$) of fecundity with Cadmium levels. Based on settlement studies, further south in New Zealand, at Port Nicholson, Wellington, it was suggested that *Austrominius modestus* releases nauplii in autumn (Ralph & Hurley 1952). Further south again, at Lyttleton, spawning may take place throughout most, if not the whole, of the year (Skerman 1958). In samples collected from Garden Island, Sydney, SE Australia, there was evidence of low levels of breeding through most the year, except January and February (see Figure 7, p. 167, Wisely & Blick 1964), but eyed embryos (maximum of 21% of barnacles sampled) were present in seven months only. Although there was some evidence that nauplii were more liable to be released during the colder months of the year, small numbers were released during most of the year. However, it is uncertain whether the specimens examined were *Austrominius modestus*, since Foster (1982) subsequently described three species of the Subfamily Elminiinae from eastern Australia.

Barnes (1989) highlighted the potential effect of salinity on the breeding season of barnacles, especially in estuarine habitats or monsoon areas, referring to species of *Balanus* and *Chthamalus*, but not *Austrominius modestus*. Moore (1944) mentioned that in their native range, *Austrominius modestus* thrive at the edge of channels in mangrove forests, but the authors are unaware of any data on how variations in salinity in this habitat may affect their breeding cycle.

Brooding season in the introduced range in Europe: The brooding season (i.e. in what months of the year embryos occur) of *Austrominius modestus* in Europe has been mentioned by a number of authors (e.g. Knight-Jones & Waugh 1949, Crisp 1954, 1957, Crisp & Davies 1955, Wisely 1960, Crisp & Patel 1961, Stubbings & Houghton 1964, Barnes & Barnes 1966, 1968a, Harms 1984, Barnes 1992, O'Riordan & Murphy 2000, Macho 2006, Macho et al. 2010, Gallagher et al. 2016), although not all of the authors were able to sample throughout the year. Although *Austrominius modestus* can reproduce at a wide range of temperatures, breeding is most rapid at moderately high temperatures (Barnes & Barnes 1962), and, similar to its native range, at some locations, brooding can occur throughout the year. However, breeding of *Austrominius modestus* becomes seasonal at the northern limits of its distribution, where sea temperatures drop below 6°C (Barnes 1992). Gallagher (2016, Gallagher et al. in prep.) recorded the percentage of *Austrominius modestus* and *Semibalanus balanoides* that had embryo masses in March and November on the Isle of Cumbrae, SW Scotland. For *Austrominius modestus*, they found that a higher percentage of individuals were brooding in September, but this never exceeded 47%. The opposite trend was seen in the cold-water *Semibalanus balanoides*, with up to 100% of individuals brooding embryos in March, with <5% in September, which, being in an early stage, would overwinter in the mantle cavity. In Helgoland, Germany, *Austrominius modestus* breeds at 7–18°C in May–October, with the main period of hatching being between mid-July to mid-September when water temperatures are 16–18°C (Harms 1984). Yet when *Austrominius modestus* is held at a constant 12°C in the laboratory, individuals breed throughout the year (Harms 1984). Crisp & Chipperfield (1948) commented that *Austrominius modestus* breeds prolifically over the greater part of the summer, while Crisp & Davies (1955) noted that a high percentage of individuals in fast-flowing water can be found brooding in warmer months in Great Britain. In the 1950s, Crisp (1957) commented that it was the only barnacle species in Britain which has egg masses from which first-stage nauplii can be obtained throughout the year, at least in certain parts of the British coast (Wisely 1960). A number of authors have examined how reproduction can vary within a geographic region, such as Wales. Variability occurs between sites, even between closely located ones, but also between years. For example, at Menai Bridge, in North Wales, *Austrominius modestus* breeds and contains nauplii all year round (Crisp & Patel 1961, Foster 1971b), but nearby at Bangor Pier, embryos were found from March–October only (Austin et al. 1958). Further south in Wales, at Swansea, (Moyse, 1960), *Austrominius modestus* produced nauplii all the year round. This was also seen by the same author a few years later, when a high percentage of *Austrominius modestus* samples collected from the piles at Mumbles Pier, Swansea, Wales, had embryos at most times of year (Moyse 1963). Based on sampling of *Austrominius modestus* during the summer months in southern England and Wales, ~two-thirds of the mature population contained egg masses (Crisp & Patel 1961). According to Southward (2008), *Austrominius modestus* breeds throughout the year in southern England, but the rate reduces in the second half of winter and early spring. Patel & Crisp (1960a) commented that most of the embryos present in late January and February on the Essex Coast were ready to hatch, but would not do so until temperatures increased. By contrast, in Chichester Harbour (West Sussex), Stubbings & Houghton (1964) noted that brooding adults, with stage I nauplii present, had been recorded in February, but this was unusual and liberation of larvae occurred from April onwards. These authors pointed out that *Austrominius modestus* needs a sufficiently high temperature at the time of fertilisation, egg-laying and spawning, with 6.0–6.5°C being the critical temperature for spawning. Ross et al. (2003) noted that it is summer breeding. Even at similar latitudes, there can be variation in reproduction on different coasts. In southern England, there is variation in breeding between the east and west coasts. In south-west England, continuously submerged specimens could be found brooding embryos even in the coldest months, but this was not the case in south-east England (Crisp & Davies 1955). In south-west England, up to 80% of continuously submerged specimens were brooding in summer months (at temperatures as high as 23–25°C at Burnham-on-Crouch), decreasing in the late autumn and winter (down to 15%–20%) (Crisp & Davies 1955). For *Austrominius modestus* on experimental plates suspended ~2 m below sea surface, Crisp & Davies (1955) found no lunar (hence tidal) periodicity in the breeding cycle, and they suggested that this may be the same case for intertidal specimens, too. Tighe-Ford et al. (1970) noted that in southern England, the larvae develop from late spring to early autumn, but a small percentage contained egg masses in January and February, that is, during the winter. Crisp & Southward (1958) stated the main breeding period of *Austrominius modestus* in the English Channel as May-October-January.

In their westerly introduced range, in southern Ireland, embryos were found throughout the year, but there was a peak in the summer, with up to 90% brooding, although there was some variation between their three sites, with the percentage brooding in the outfall site being significantly lower (O'Riordan & Murphy 2000). Murray (2009) recorded a maximum of 53.3% of the sampled *Austrominius modestus* brooding embryos in June 2009. Similarly, Gallagher et al. found embryos in all but one month in Bullens Bay, Co. Cork, Ireland, in 2014–2015, but the level of brooding varied during the year (see Figure 3). The only other published data for Ireland are from further north.

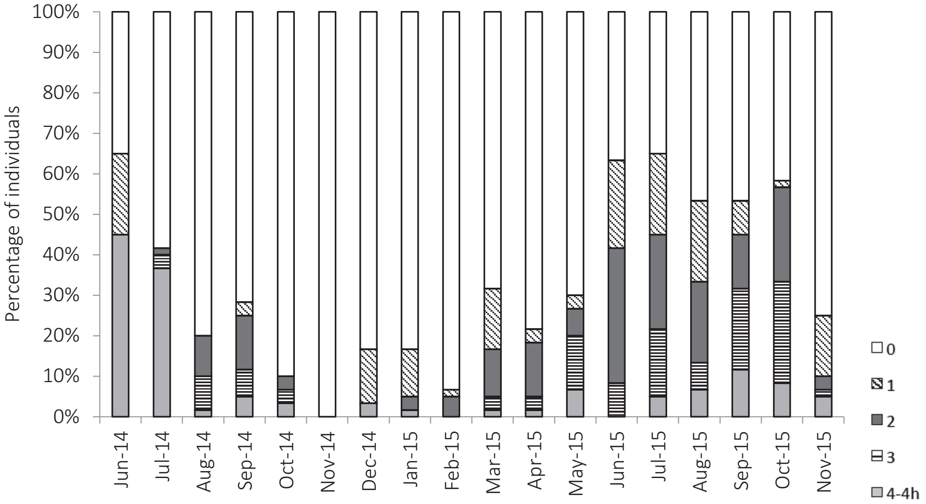

Figure 3 Percentage of *A. modestus* brooding embryos in different stages of development from Bullens Bay, Co. Cork, Ireland, in 2014–2015. Key on right-hand side of figure shows stage of development, from stage 0 (white) to stage 4-4h (stippled), using the scale of O'Riordan & Murphy (2000).

In Donegal, up to 45% were recorded brooding in June (O'Riordan 1996), but only a maximum of 28.5% in Galway Bay, between February and April (King et al. 1997).

Barnes (1992) described the breeding seasons of a number of species of barnacle in different parts of their range; however, the only location for *Austrominius modestus* was from Arcachon Bay in France, where she carried out sampling irregularly for several years beginning in 1965 ($n = 50–450$). All of the sampled *Austrominius modestus* had fertilised embryos in January and March, with nearly 100% in December (Barnes 1992). Barnes (1992) suggested that the high percentage in winter represented a population synchrony, following an autumn minimum, which may have been due to peculiar local nutrient conditions or greater competition for the amount available at this site. Synchronous breeding at this site was further supported by the release of all of the embryos in March and April and a low level or absence of egg masses during May and June. A reduction in body weight in April was suggested to be due to the barnacles not continuing to breed then, even though temperatures were much more favourable to gonadal development than in the winter. This may be a result of the local low nutrient conditions or greater competition for the available food. The body weight increased from April to June when a second brood was initiated, giving rise to a new maximum of gravid animals in July and August and consequent loss in body weight. The only other records of timing of reproduction in France and how it may vary with location were collected during surveys monitoring the spread and changes in abundance of *Austrominius modestus* on the continental coast (Barnes & Barnes 1965b, 1966, 1968b). Barnes & Barnes (1965b, 1966) reported only low levels of brooding, despite sampling in midsummer; for example, in Brittany, France, they found 0% brooding at St. Quay Portrieux (11th June), but egg masses were present at Port Blanc (15th June) and at Pornic on 16th June and 15th September 1963. Ten percent had egg masses at Ribadeo, Spain (3rd July 1963). In their survey of the French coast in 1967, some sites showed higher levels than four years previously, which may be because sampling was two months later (August). Barnes & Barnes (1968b) recorded the following percentages with egg masses: 25% at Talmont and in the Arcachon Basin, between 2% (on piles at La Jetée d'Eyrac) and 19% at Arcachon, 33%–50% at Port de Larros, 10% at Cassy, 17% at Arès, 32% at Bélisaire, 50% on pignots in Sableyre de Comprian and 15% at Pyla-sur-Mer. At Petit Nice, on exposed concrete blockhouses, south of the dunes at Arcachon, many of the *Austrominius modestus* had developing embryos in April 1971 (Barnes et al. 1972). Further south, in Ria de Arousa, NW Spain, it has been reported that *Austrominius modestus* can breed throughout the year (Macho 2006, Macho et al. 2010). Other species overlapping in the introduced range of *Austrominius modestus* in Europe may also have embryos present during the winter months, but the level of brooding is lower than when there are higher temperatures. At the known southern-most limits of its European range, (Gallagher, 2016, Gallagher et al., in prep.) recorded the percentage of *Austrominius modestus* that had embryo masses in February and August at Farol, Ihla de Culatra, Algarve, Portugal, as well as the percentage with different stages of egg development weekly over a four-week period in July-August, in comparison to the native *Chthamalus montagui* Both species had embryos present in February and August, but the levels of brooding were higher in *Austrominius modestus* (maximum = 67%). For both species on all four dates in July-August, stage 4 and 4 h embryos were present, but *Austrominius modestus* had a higher percentage of these, as well as having up to 85% with egg masses versus only 53% in *Chthamalus montagui*. O'Riordan & Ramsay (1999) reported that 60% of their sampled *Austrominius modestus* from Praia de Faro contained embryos in April.

Moyse (1963) linked the longer breeding season of *Austrominius modestus* (than *Semibalanus balanoides* and '*Chthamalus stellatus*') to the former's more catholic feeding habits. The larvae of *A. modestus* can be reared on both diatoms and flagellates, unlike the two other species. *Semibalanus balanoides* were reared successfully on diatoms, but not flagellates and vice versa for '*Chthamalus stellatus*', which is linked to their different geographic distributions and that of available food. These three species have distinct ranges in egg size, which has implications for the naupliar size and on the size of the phytoplanktonic species on which they feed in the wild (Barnes & Barnes (1965a).

Breeding and anthropogenic effects of temperature and salinity: In their introduced range, *Austrominius modestus* can be found in large numbers in estuarine areas, but the only published comparison of breeding in different salinity conditions in the field is that mentioned previously (O'Riordan & Murphy 2000). In southern Ireland, a significantly lower percentage of *Austrominius modestus* were brooding at their site of a warm-water outfall from a power station, where a wide range of salinities were recorded, than at another site nearby (O'Riordan & Murphy 2000). In contrast, Pannell et al. (1962) reported that the breeding season of *Austrominius modestus* was prolonged and extended into autumn in parts of Southampton water, which they suggested may have been a result of elevated warmer water conditions due to the activity of the Marchwood Power Station.

Variation in the number of broods

Although *Austrominius modestus* can have multiple broods per year, only a few publications have examined the number of broods in detail. Crisp & Davies (1955) pioneered the use of glass slides to examine *in vivo* the breeding of this species, which is possible because the embryo masses could be seen developing, as this species has a transparent membranous base. It would be useful to use similar methods to examine the age of first brooding and number of broods/year in other parts of *Austrominius modestus*'s introduced range, as well as in Australasia. This would be especially interesting at the current northern and southern limits of its introduced range. The range limits may be controlled by cold temperatures and out-competition by arctic-boreal barnacle species, but potentially lowered fecundity and desiccation effects on cyprids, metamorphs and maybe adults, at least intertidally, at the northern and southern limits, respectively.

Crisp & Davies (1955) described how reproduction in *Austrominius modestus* is characterised by a succession of broods, with the time taken for each brood to develop varying between individuals and season, with temperature being the main controlling factor. They estimated that in Great Britain, subtidal *Austrominius modestus* may produce 12 broods per year (but see subsequently), which is very different to the cold-water species *Semibalanus balanoides* and *Balanus balanus*, in which individuals only produce one brood per year. Other species (e.g. *Chthamalus stellatus* and *C. montagui*) overlapping in the introduced range of *Austrominius modestus* in Europe may also produce multiple broods per year. However, the maximum number of broods per year was usually two in 1+ individuals (O'Riordan et al. 1992), but zero to two in their first summer after settlement. This was seen through following individuals using experimental plates similar to Crisp & Davies (1955), rather than calculating based on the state of the gonads or embryos in a population. Crisp & Patel (1961) estimated that between mid-July until December, their experimental subtidal *Austrominius modestus* population in Menai Straits, Wales, could have 8 to 10 broods. They noted that the last brood of the season for a 0+ individual would be the heaviest. In western Scotland, where temperatures are only moderate (maximum 15–16°C), in its first year, *Austrominius modestus* may only produce one or two broods and only two or three broods per year in subsequent years (Barnes & Barnes 1962). However, further south, in Ria de Arousa, NW Spain, where it has been reported that *Austrominius modestus* can breed throughout the year, it was estimated that it can produce 18–22 broods per year (Macho 2006, Macho et al. 2010).

Fecundity

Austrominius modestus shows great/remarkable fecundity (Knight-Jones & Waugh 1949, Crisp & Davies 1955) or prolificacy (Darwin 1854, Moore 1944, Bishop 1947, Knight-Jones 1948). To date, little work has examined fecundity of *Austrominius modestus*, but no difference was found from Scotland to Portugal (see details subsequently). It is known that *Austrominius modestus* has smaller broods than many other barnacle species, but this may be compensated by producing multiple broods per year. In crustaceans, the number of eggs carried by a parent at any one time is a function of the size of the parent, but in barnacles it varies also with age, food supply and crowding. Barnes & Barnes (1968b) defined barnacle fecundity as the number of eggs produced per given increase in weight of the adult (slope of the adult size – egg number regression) per unit time. For *Austrominius modestus* (based on collections for Stranraer, Ribadeo, Silloth, Portosin, Pornic, Pontevedra, Croix de Vie and Nazaré), Barnes & Barnes (1968b) gave this as 1800 eggs per 1.0 mg dry body weight. This weight represented a moderate-sized individual. No significant differences in fecundity between site or region were found for *Austrominius modestus* (from Scotland to Portugal) and four other barnacle species (*Amphibalanus amphitrite, Perforatus perforatus*, *Euraphia depressa* and *Pollicipes cornucopia*), unlike their results for *Amphibalanus improvisus*. They suggested that the lack of variation was because the first five species occur in a relatively narrow range of ecological conditions, so egg production is similar.

In order to compare the reproductive efficiency of different barnacle species which may vary greatly in adult size, Barnes & Barnes (1968b) suggested using the number of eggs produced per increase of 50 µg dry body weight (N). This can be multiplied by the egg volume (V) to give the product ($N \times V$), which can be multiplied by the number of broods (B), when known, to give the metabolic efficiency of egg production (NVB) (the rate at which a given increment of body weight produces egg tissue). For *Austrominius modestus*, using samples collected from Stranraer, Scotland, they multiplied the number of eggs per increase of 50 µg dry body weight (87.5) by an egg volume of 2.05×10^{-6} mL, giving a product of 179. These authors then used Crisp & Davies (1955) data for *Austrominius modestus* living on continuously submerged plates, with presumably excellent nutritional conditions. If 14 days is assumed the minimum time required to produce a brood, some 26 broods could be produced a year; giving a NVB of 4654 (i.e. 26 × 179). When this value was corrected to compare with the eight-month period of brooding of *Semibalanus balanoides*, the metabolic efficiency of egg production was similar. However, because the eggs of *Austrominius modestus* are much smaller than those of *Semibalanus balanoides*, *A. modestus* produces more nauplii per unit weight of egg tissue. Crisp (1987) pointed out that a small brood size may be counterbalanced by warm-temperate species being able to produce multiple broods. Barnes & Barnes (1968b) noted that the smaller eggs of *Austrominius modestus*, which are produced in successive though smaller broods, can settle and reach maturity quickly and so contribute to further egg production, giving this eurythermal species a tremendous advantage over *Semibalanus balanoides*. This is one of the mechanisms facilitating its initial rapid spread. The potential ability to produce larvae over a longer period of the year than *Semibalanus balanoides* is also advantageous (Leloup & Lefevere 1952).

Crisp (1960b) suggested that the high temperatures and prolonged summer that occurred in 1959 in Great Britain may have allowed individuals to breed for a longer period of the year, resulting in increased fecundity. Greater fecundity boosted the spread of *Austrominius modestus* on both the east and west coasts, including the Firth of Clyde, Scotland, towards its northern limit, after little change in the previous five years.

Barnes & Barnes (1968b) pointed out that when comparing the overall egg production of different species and the potential competition for space on the substratum, it is necessary to consider the size (age) structure of the population as well as other factors. Also, they suggested that within the littoral, *Austrominius modestus* broods much less frequently than the every 14 days seen in the sublittoral. Barnes et al. (1971) estimated that in Arcachon, France, egg production of *Austrominius modestus* was 6.26 g dry weight per m^2 surface area per year.

With respect to fecundity over a lifespan (although how long *Austrominius modestus* lives in different conditions is not known yet), Crisp & Davies (1955) estimated that if *A. modestus* lives for three breeding seasons, having an average number of 500 nauplii in each brood, and 12 broods per season, the total output of nauplii would be ~18 000 per individual.

Crowding and food supply: Another factor affecting reproduction is when crowding among individuals reduces food supply. In laboratory conditions, fecundity increased with access to unfiltered, flowing seawater, but when starved, no fertilisation occurred and release of larvae was delayed (Crisp & Davies 1955). Even so, the normal cycle resumed a few weeks after being returned to non-filtered seawater (Crisp & Davies 1955). Crowding (and thus less available food) delayed the onset of breeding, but egg masses were found in smaller *Austrominius modestus* (but of about the same age) than in uncrowded individuals (Crisp & Davies 1955, Crisp & Patel 1961). According to Crisp (1959a), Clegg (unpublished observation) found that eggs of *Austrominius modestus* developed from a fairly early stage (Stages 5–9, Crisp 1954) in seawater *in vitro* without difficulty and hatched.

Barnacle age, size and egg production: As mentioned previously, *Austrominius modestus* can start breeding at a very young age, but Barnes (1989) pointed out that age can also affect the number of eggs produced. Crisp & Patel (1961) suggested that for a given weight, the weight of egg masses and number of eggs was less in small (younger) barnacles than in larger (older) ones. Crisp & Davies (1955) said that their subtidal experimental *Austrominius modestus* approached maturity at a RCD of 4–7 mm, but they found that under experimental conditions, those with a RCD measuring >6 mm were more fecund (i.e. bred more frequently) than those between 5–6 mm, which in turn were more fecund than those between 3–5 mm.

Sterility and age: Unlike some other barnacle species, there is no evidence to suggest that fecundity of *Austrominius modestus* decreases with age. Crisp & Davies (1955) reported that at least some subtidal *Austrominius modestus* in their third summer contained embryos, and there was no significant difference in breeding behaviour when compared with younger, but mature, individuals. This is despite the fact that at this age, they would have already produced 30–40 broods. They pointed out that a similar lack of sterility with age had previously been seen in *Balanus balanus*, but *Semibalanus balanoides* does show sterility (Moore 1935).

Moulting and breeding: The relationship between breeding and ecdysis has been examined under laboratory conditions for a number of acorn barnacle species, including *Austrominius modestus* (Crisp & Patel 1958). All of the species studied had a prolonged intermoult period when the barnacle had embryo masses present, but still moulted. For *Austrominius modestus*, similar to three other species studied (*Balanus crenatus*, *Perforatus perforatus* and '*Chthamalus stellatus*') where embryonic development is relatively fast, especially at higher temperatures, normal moulting resumed shortly after incubation. The moulting rate was dependent on food supply and temperature, but the normal intermoult period for these species was only 6–10 days. However, Patel & Crisp (1961) gave similar intermoult periods for *Balanus crenatus* (11–13 days at 10–11°C) and *Semibalanus balanoides* (10–12 days at 8–12°C) but only 6 to 7 days (at 14–16°C) for *Austrominius modestus*. In *Austrominius modestus* and *Balanus crenatus*, there was no detectable influence of the moulting phase on the frequency of copulation (and hence fertilisation), and this occurred with equal ease at any time of the cycle, which was different to *Semibalanus balanoides*. Patel & Crisp (1961) reported that very few *Austrominius modestus* moulted 24 hours before liberation, but during the period 12–24 hours after liberation, the moulting rate was very high. When unfertilised, the intermoult period of *Austrominius modestus* was an average of 5.4 days, while this was 15.2 days if starved. If fertilised, the intermoult periods of *Austrominius modestus* only varied by a day (15 if fed versus 16 if starved), although the latter small difference was not seen in *Balanus crenatus*. In the laboratory, the moulting rate increased linearly from 4 to 23°C and was similar whether the animals were well fed or starved. The latter also occurred in *Perforatus perforatus*, but this pattern was not observed in starved '*Chthamalus stellatus*' and *Amphibalanus amphitrite* (Patel & Crisp 1960b).

Egg shape and size

Crisp (1987) reviewed the shape and size of eggs of cirripedes and suggested that both may be useful as taxonomic characters. Barnes (1989) described the shape of fertilised eggs of barnacles as ovoid, with the width being narrower at one end, giving a tapering shape, which Crisp (1987) called 'typically pyriform'. The shape (length/breadth) changes from egg through to stage VI nauplius, which is similar in *Austrominius modestus* as a range of *Balanus* species (Crisp 1987). Table 2 shows data from Crisp (1987) on the shape of *Austrominius modestus* eggs and nauplii. There are differences between the species that produce lecithotrophic versus planktotrophic larvae (i.e. *Austrominius modestus*), with the former having much more globular eggs, but usually fewer in number in a brood (Barnes 1989).

At least five independent factors influence variation in egg size within a species of cirripede (see Crisp 1987, for a detailed discussion): stage of development, temperature, genetic differences, individual variation and also variation within an egg mass (Crisp 1987, Barnes 1989). The greatest amount of information is available for the arctic-boreal *Semibalanus balanoides*, especially with respect to genetic, individual and environmental factors other than temperature. The size of eggs of warm-water species (that can breed continuously above a critical temperature when plenty of food is present) is greatly influenced by temperature (Patel & Crisp 1960b, Crisp 1987). Most of the published data (see Table 3) for egg size in *Austrominius modestus* gives the dimensions of the mature egg (stage 4 embryo) before it has hatched (stage I nauplius). Crisp (1976) flagged that the volume of unhatched stage 1 nauplii will be smaller than that of the hatched stage I nauplii, since the nauplii are tightly packed inside the egg case. For *Austrominius modestus*, Crisp (1987) gives an egg volume of 1.53×10^{-6} mL for the maximum size before release. This egg volume is relatively small and is in line with other warm-temperate species, which is linked to the higher environmental temperature and also the small size of the adult and hence the mantle cavity (Crisp 1987). Patel & Crisp (1960b) showed the sizes of eggs at all stages of development: from stage 1 (early development, from newly laid to a few cells), 2 (multicellular) to 3 (from the appearance of limb buds to the presence of limbs and spines), to stage 4 (nauplii eye present to hatching, 4 h) under different temperature regimes in the laboratory (see Table 3). They found that all four of the southern/warm-water species tested ('*Chthamalus stellatus*', *Amphibalanus amphitrite* var. *denticulata*, *Perforatus perforatus* and *Austrominius modestus*) produced larger embryos from ova when maintained experimentally at low temperatures than they do at high temperatures. They attributed this to different rates of

Table 2 Shape S (= Length/Breadth) of the egg and stage I–VI nauplius of *A. modestus*, according to Crisp (1987, Table II, p. 5) (line 1) and Foster (1967b) (line 2)

Egg	Nauplius I	Nauplius II	Nauplius III	Nauplius IV	Nauplius V	Nauplius VI
2.040	2.000	2.480	2.050	1.920	1.810	1.820
–	2.08	2.36				

Table 3 The resultant mean (±SE) length (mm), breadth (µm) and volume of eggs of *A. modestus*, from stage 1–7 and to 8–13, when parents, which were fed, were kept under different temperature regimes in the laboratory (based on Table 4 of Patel & Crisp, 1960b).

	Stage 1–7*			Stage 8–13*		
Mean T.	Length	Breadth	Volume	Length	Breadth	Volume
9°C	214±2.6	107±0.84	1.28	241±4.00	120±2.60	1.82
15°C	202±1.7	102±0.65	1.10	232±1.80	112±0.86	1.53
20°C	189±5.8	97±0.50	0.93	226±1.25	113±0.78	1.51
25°C	184±1.4	94±0.50	0.85	214±1.25	109±0.80	1.33

*See Crisp (1954) for detailed description of stages of eggs, but in 1–7, the egg is early stage, up to the yolk being divided with three to six or more yolk cells, (~stage 1–2 of O'Riordan & Murphy, 2000) while the egg in stage 8–13 is from the appearance of limb buds to the hatching of the larvae (~ stage 3–4 h of O'Riordan & Murphy, 2000).

differentiation, with slower rates at lower temperatures resulting in a larger size and vice versa. The volume of embryos increased from early to late development, mostly due to increasing length.

For cold-water, arctic-boreal acorn barnacle species, fertilised embryos decrease in size with decreasing latitude, that is, from colder to warmer waters (Crisp 1954, 1959a). The embryos of the arctic-boreal *Semibalanus balanoides* were larger where winters were severe and summers relatively cold, irrespective of the latitude (Barnes & Barnes 1965a). They suggested that the change of egg size within a warm-water or eurythermal species over a similar latitudinal range is much smaller than for *Semibalanus balanoides*, which they attributed partly to the rapid breeding cycle, so that any given generation of eggs is subjected to the effect of temperature for only a short time, which would be the case for *Austrominius modestus*.

To remove any influence on the early stages of development prior to fertilisation, Patel & Crisp (1960b) transferred fertilised eggs, at early, middle and late stages of development, from three parents. They then examined the effect of three different temperatures on subsequent stage I nauplius size (length, breadth and derived volume) of released naupliar stage I when embryos were incubated *in vitro*. They suggested that temperature affected both the ova and subsequent embryo and hence naupliar stage I size. Although there was variation in nauplius size, even within a brood, Patel & Crisp (1960b) reported that those that developed *in vitro* at the highest temperatures (23°C) resulted in the smallest nauplii I, and those transferred at the earliest stage resulted in the greatest loss in volume (see Table 4), which Crisp (1987) attributed to an increase in metabolic rate resulting in extra consumption of reserves. For *Austrominius modestus*, O'Riordan & Murphy (2000) found that eggs within a brood were all at the same stage of development, which they attributed to the relatively small and thin egg mass, which, as suggested by Patel & Crisp (1960a), may allow uniform development.

Larval stages

Austrominius modestus has six naupliar stages, followed by a single cypris stage, which is adapted morphologically for site selection and settlement. The stage I nauplius, which is non-feeding (Foster 1967b) and moults to the stage II nauplius, occurs for a very short time only, from just a few hours (Foster 1967a), to 24 hours in the laboratory (Knight-Jones & Waugh 1949). The maximum length of time that an individual naupliar larva of *Austrominius modestus* can remain in the water column before metamorphosing into the non-feeding cypris stage is unknown, but the minimum time from stage I nauplius to cyprid has been calculated for laboratory-reared larvae to be six days (see e.g. Moyse 1963, Foster 1967a,b, Barker 1976). Combining his data on rearing larvae in the laboratory and long-term temperature data, Harms (1984) predicted the duration for the larvae to develop into

Table 4 Influence of temperature on mean (±SE) length (μm) and breadth (μm) of resultant stage I nauplii of *Austrominius modestus* when the fertilised eggs, at different stages of development, have been removed from individual parents and then reared *in vitro* at 11, 16 or 23°C

		11°C		16°C			23°C		
Parent no.	Stage of egg*	Length	Breadth	Length	Breadth	% Loss	Length	Breadth	% Loss
1	3–4	268±1.5	116±0.5	252±2.5	115±0.6	7.7	229±3.9	108±1.3	26.0
2	6–7	259±1.1	118±0.9	247±2.6	114±0.8	11.0	232±5.6	112±1.4	20.0
3	8–9	260±1.1	118±1.2	252±2.0	119±2.4	1.0	246±0.5	114±0.7	12.0

Note: Stage = stage of development* of transferred eggs at the start of the experiment, % loss = percentage loss of volume of eggs in comparison to egg developed at 11°C (based on Table 5 from Patel & Crisp 1960b) and Table VI from Crisp (1987).
*See Crisp (1954) for detailed description of stages of eggs, but in 3–4, the yolk is undivided, and in 6–7, the yolk is divided with three to six or more yolk cells, while 8–9 is from the appearance of limb buds to the presence of limbs, but the setae are absent or not evident.

cyprids in the wild in the Helgoland area. He suggested 30 days in spring, but only 14 days in August. Since they have a shorter planktonic life, the larvae of species of barnacle that inhabit relatively sheltered areas, such as *Austrominius modestus*, have smaller larvae than species from oceanic and exposed coastal areas (Moyse 1963).

Numerous authors have reared the nauplii of *Austrominius modestus* in the laboratory, and a smaller number describe how to rear the cyprids. Subsequently we discuss some of the most important findings arising from this work, focussing on variations in rates of development and survival using different diets, temperatures and salinity, as well as how these affected the size of the resultant nauplii, cyprids and metamorphs.

Nauplii

Description of the nauplii

Knight-Jones & Waugh (1949) were the first authors to describe the morphology of the larvae of *Austrominius modestus*, based on the hatching in the laboratory of stage I nauplii which had been obtained from adults and from plankton samples. They measured the total length, greatest breadth of nauplii and carapace length (including length of spines). When a carapace fold was present, they found that the greatest breadth was the most useful measurement for identifying the various naupliar stages, since the carapace length is affected by the degree of flexure of the abdomen. They gave the setation formulae for the antennule, antenna and mandible for all six naupliar stages (see Table 5), accompanied by detailed drawings and the description of the naupliar stages. They described how a combination of the size, shape, limb setation and labrum of the naupliar stages could be used to distinguish *Austrominius modestus* from the larval stages of other barnacle species occurring in British waters. A very useful key for the identification of stage II–VI nauplii of common barnacles of the British Isles is that of Ross et al. (2003), who used Knight-Jones & Waugh's (1949) descriptions and measurements of *A. modestus*. They pointed out that although both *Austrominius modestus* and *Perforatus perforatus* nauplii have a trilobed labrum, those of the former can be distinguished by the fact that the medial lobe of the labrum extends out much further than the two lateral lobes (in comparison to only slightly in *P. perforatus*), as well as other differences, for example, in cephalic shield size and shape and the stubby frontolateral horns in stages IV–VI. Ross et al. (2003) included scanning electron microscopy (SEM) of the ventral surface and the medial lobe of the labrum of a stage VI nauplius of *Austrominius modestus*.

In order to be able to identify the larvae of different species of barnacle in the water column by morphology, it is necessary to rear them in the laboratory to be sure of the parentage and then

Table 5 Setation formula (follows Bassindale 1936) of the appendages of the nauplii of *Austrominius modestus* reared by Barker (1976) from adults collected in Leigh, Auckland, New Zealand, based on his Table 2

Stage	Antennule	Antenna	Mandible
I	0.**4**.2.1.1	0.**1**.4–0.**3**.2.2.2.G	0.**1**.3–0.**3**.2.2.2.G
II	0.**4**.2.1.1	0.**2**.5–0.**3**.2.2.3.G (0.**1**.6–0.**3**.2.2.3.G)	0.**1**.3–0.**3**.2.2.2.G
III	1.**4**.2.1.1	0.**2**.5–0.**3**.2.2.4.G (0.**1**.6–0.**3**.2.2.4.G)	0.**1**.4–0.**3**.3.3.3.G
IV	1.1.**4**.2.1.1	0.**2**.7–0.**5**.3.2.4.G	0.**1**.4–0.**4**.3.3.3.G
V	1.1.1.**4**.2.1.1.1 (2.1.**4**.2.1.1.1)	0.**3**.8–0.**5**.3.2.4.G	0.**1**.5–0.**4**.4.4.3.G
VI	1.1.1.**4**.2.1.2.1 (2.1.**4**.2.1.2.1)	0.**4**.8–0.**5**.3.2.4.G	0.**1**.5–0.**4**.4.4.3.G

Note: Bold numbers refer to terminal setae. The formulae on brackets are those differences found by Knight-Jones & Waugh (1949), which are explained in the text below.

describe their main characteristic features. Stage I and II nauplii of *Austrominius modestus* and six other species from New Zealand samples, reared in the laboratory from stage I nauplii taken from the mantle cavity of adults, were described by Foster (1967b). A combination of features, such as carapace shape and length/width ratio, as well as form of the labrum, allow these different New Zealand species to be distinguished. Following on from the work of Knight-Jones & Waugh (1949), Foster (1967b) noted that the labrum of stage II nauplius of *Austrominius modestus* with its distinct protruding middle lobe and relatively short but forwardly facing front-lateral horns are distinguishing characteristics from other New Zealand species. Subsequently, Barker (1976) reared all of the naupliar stages (and cyprids) of six of the same species (including *Austrominius modestus*) and developed a key to distinguish between the nauplii of these species. Although Knight-Jones & Waugh (1949) had described the larvae of *Austrominius modestus*, they were from European adults. In the New Zealand specimens, Barker (1976) mentioned some differences in setation from earlier descriptions; however, this was probably due to a different interpretation of what constitutes a group of setae, rather than a structural difference in the larvae (Barker, 1976), as the text diagrams of Knight-Jones & Waugh (1949) indicated identical setation to New Zealand nauplii (see Table 5). Egan & Anderson (1985) suggested that some of the discrepancies, with respect to larval setation between Knight-Jones & Waugh (1949) and subsequent authors, may be also a consequence of different techniques of microscopy. For instance, Jones & Crisp (1954) noted the presence of a spine on the endopod of the mandible in *Austrominius modestus* larval stages collected in the plankton from four southern British estuaries and an extra seta in the form of a stub on the mandibular exopod in stage II nauplii of *A. modestus*, which were unreported by Knight-Jones & Waugh (1949). It is also possible that phenotypic traits are polymorphic at different locales.

In summary, Barker (1976) (p. 145 therein and Figure 6, Tables 2 and 3) succinctly describes the distinguishing features of the nauplii of *Austrominius modestus* as 'Carapace triangular, length less than twice the width. Short posterior spines present in IV–VI. Short fronto-lateral horns directed anteriorly in II–VI. Frontal filaments present in stages II–VI. Abdominal process and caudal spine weakly developed in I, the former half the length of the latter in II, two-thirds the length in IV–VI. Labrum trilobed, with a median lobe extending well beyond lateral lobes'.

The paper on larval development of *A. covertus* and *Hexaminius popeiana* includes a useful table describing the features that can be used to distinguish stage II, IV and V nauplii of *A. covertus* and *Austrominius modestus* as well as the nauplii of *H. popeiana* when they co-occur in Australian waters (Egan & Anderson 1985), but there were no known distinguishable differences between stage I nauplii or the cyprids, and the limb setation has to be examined to distinguish their stage III nauplii.

Frontal horns, filaments and sensory function: Walker (1973, 1974) described the frontal horns and associated gland cells and the frontal filament complexes of the nauplii of *Austrominius modestus*, *Chirona hameri* and *Semibalanus balanoides*. The frontal horns of naupliar stages I and II *Austrominius modestus* are only about a third of the size of those of *C. hameri*, but they have a similar external appearance and have ventral perforations, while those of *Semibalanus balanoides* are much shorter and lack the perforations. However, for the three species, the associated gland cells of all naupliar stages and the frontal horns of naupliar stages III–VI are morphologically similar.

The frontal filaments have a pressure and/or orientation sensing function (Walker 1974). Stage I nauplii are strongly photopositive at liberation (Wisely 1960), and this is still the case for stage II nauplii of *Austrominius modestus* (Crisp & Ritz 1973). The latter authors showed the loss of dark adaptation of stage II nauplii of *Austrominius modestus* when subjected to white light in the laboratory. Tighe-Ford et al. (1970) had noted that nauplii are positively phototactic and, subsequently, Barnes & Klepal (1972) determined the spectral sensitivity of the naupliar eye of dark-adapted stage I nauplii of *Austrominius modestus* and *Semibalanus balanoides* and found maximum sensitivity for positive phototaxis between the wavelengths of 520–530 nm (blue-green). The photic response of the cyprids of *Austrominius modestus* is particularly interesting, since this species can settle both intertidally and sublittorally.

Use and effects of different culture conditions on naupliar development

Temperature, diet and salinity

Different culture conditions, in particular temperature, diet and salinity, affect rates of development, survival and the resultant size of the larvae. Moyse (1960), working in Swansea, Wales, noted that *Austrominius modestus* larvae in the laboratory can tolerate considerable fluctuations of temperature. At 20 ± 3°C, when *Austrominius modestus* nauplii were reared using different species and densities of flagellates and diatoms, a unialgal diet of the diatom *Skeletonema costatum* was found to be very successful, but nauplii fed on the diatom *Phaeodactylum closterium* took longer to develop, while those fed certain species of flagellates seemed to have thin cuticles and were unable to moult properly (Moyse 1963). A link between the geographical distribution of barnacle species and the diet of the larvae is possible, with those of cold-water species (with widely spaced setules) developing well on diatoms, while those of warm water (with a fine-meshed filter) develop better on flagellates (Moyse 1963). According to Stone (1989), *Austrominius modestus* has an intermediate distribution, so the larvae can survive on both larger diatoms and smaller flagellates, which may facilitate breeding and larval production throughout the year. However, *Austrominius modestus* larvae survived better on diatoms at cooler temperatures, but at warmer temperatures, flagellates promoted survival. By contrast, the nauplii of *Semibalanus balanoides*, whose larvae are released in spring, do better on diatoms (Stone 1986). Anderson (1994) pointed out that the retention of a moderate mesh size of 3–4 µm on the basal antennal setae of the nauplii of *Austrominius modestus* and *Perforatus perforatus* allows them to exploit a mixed diet.

Stone (1986, 1988, 1989) carried out some of the most detailed experiments using six different feeding regimes and different diets for the nauplii of *Austrominius modestus*, examining how these affected the rates of development and survival, as well as the sizes of the resultant nauplii (culture temperature was 18 ± 0.2°C, with a salinity of 35). Development was fastest when nauplii were fed a uniagal diet of the small flagellate *Isochrysis galbana* for the first four days, followed by a uniagal diet of the larger flagellate *Rhodomonas* sp. from days five to nine, but a mixed diet of these two species throughout gave higher survival (Stone 1988). These differences may be due to an increase in the mesh size of the antennal filter during growth of the nauplii. Stone (1988) reiterated the importance of the antennal endopodite for feeding in the nauplii and that the intersetular distances affect what size of particles can be captured. Of the total area covered by setae on the endopodite, there was a greater coverage of finely spaced setules (<5 µm apart) in the stage II (36.3 9%) vs stage VI (13.92%) nauplius of *Austrominius modestus*. The closest intersetular spacing on the antenna in stage II *Austrominius modestus* was 2 µm, with some spaced 3 or 4 µm apart in stage II and VI, but with the maximum spacing being 13 µm (see Figure 3, p. 26, Stone 1989). These results supported the suggestion that nauplii collect their food by means of filtering appendages rather than by localised currents alone, with the larvae selecting larger-sized particles as they grow (Stone 1988, 1989). Significant differences in carapace length and width of Stage IV and V nauplii occurred when they were fed different diets, with larger larvae resulting when larger algal cells were fed in the later stages of development (Stone 1988). According to Stone (1989), Walker et al. (1987) observed nauplii of *Austrominius modestus* (and *Semibalanus balanoides*) when they were restrained and found that the feeding mechanism relied on the recovery stroke of the antennae, which brought food particles within reach of the mandibles on their backward stroke. The mandibles then pushed the particles towards the labrum. In her test of ten different diets for *Austrominius modestus* nauplii, Stone (1989) found that diets containing the dinoflagellate *Prorocentrum micans* resulted in deformities of the ventral thoracic process in stage IV–VI nauplii.

The previous experiments comparing different diets used constant temperatures, while other authors tested the effects of a number of temperatures on the rate of development of the nauplii of *Austrominius modestus*. In the laboratory, nauplii develop at different rates depending on the temperature, but there is conflicting evidence as to what temperature is best, which may be linked to where the adults are collected. In their native range, Barker (1976) collected adults from the Leigh area, Auckland, New Zealand, and used *Skeletonema costatum* to rear *Austrominius modestus* and tried three different temperatures (20, 25 and 30°C). All six naupliar stages were cultured at 25°C, but the culturing took longer than at 20°C (e.g. stage VI after eight days vs five days at 20°C), and only the first two stages appeared at 30°C. Tighe-Ford (1977) had also successfully reared nauplii at 20°C, using *S. costatum*. In their introduced range, Harms (1984) reared larvae from stage I nauplii taken from adults that were collected in the intertidal of Helgoland. In contrast to Barker (1976), of the four constant water temperatures tested (at a salinity of 31–33), it was at the highest experimental temperature (24°C) that the larvae of *Austrominius modestus* developed quickest (~seven days) and showed the lowest mortality, although 24°C could be close to the nauplii's upper temperature limit (Barker 1976), since Tighe-Ford et al. (1970) had found 23°C to be lethal for the nauplii of *Austrominius modestus*. The ingestion rate of *Austrominius modestus* larvae has been found to increase with temperature (Harms 1987), maximum ingestion rate of the nauplii occurring at alga concentrations of >100–150 μl^{-1} (Yule 1986).

Temperature and swimming activity of Austrominius modestus nauplii

Temperature affects the swimming activity of *Austrominius modestus* nauplii reared in the laboratory, with their limb beat movements changing when food is present (Yule 1984, 1986). The rate of limb beat of stage II nauplii of *Austrominius modestus* was 7.2 beats per second at 20°C (Yule 1984) (see Anderson 1994, Table 8.2 for a comparison with 14 other barnacle species), while the mean limb beats per second of stage IV nauplii increased from 5 to 30°C, with a twofold increase from 5 to 15°C (i.e. a Q_{10} of 2.00). From 5 to 25°C, *Austrominius modestus* spent a greater percentage of time swimming (in the tested 5-min periods) than *Semibalanus balanoides* and *Chirona hameri*, with greater disparities as the temperature increased. At the lower temperatures, some of the *Austrominius modestus* were swimming continuously for the 5 minutes, showing no significant difference in the percentage time swimming even when monitored for six (at 20°C) to seven (at 15°C) hours. The average swimming stroke rate of *Austrominius modestus* decreased slightly as the temperature and limb beat frequency increased, which Yule (1984) suggested may, along with its eurythermy, have aided the colonization of north-temperate shores by this species that originated in the subtropical waters of New Zealand.

Size of the nauplii

The size of the adult of a barnacle species affects the size of ova and embryos, which then follows through to the naupliar size (Barnes & Barnes 1965a). Since size may be used to initially distinguish the nauplii of *Austrominius modestus* from those of other barnacle species, it is important to consider how size may vary depending on the laboratory rearing conditions and be aware that size (and colour) of cultured larvae may differ from 'wild' larvae collected from the plankton (Barker 1976). Small stage I and II naupliar larvae (measuring 110–140 μm (length including spines of 240–260 μm, respectively), as well as a few measuring 150–170 μm (length including spines of 360–430 μm), were obtained only from the laboratory (from adults collected in southern England) (see Table 6a) (Knight-Jones & Waugh 1949). Larger larvae of *A. modestus* were produced at lower temperatures (10°C vs 20°C) in the laboratory, although they took longer to develop (see Tables 1–3 of Tighe-Ford et al. (1970), for measurements and Table 4 for a comparison with Knight-Jones & Waugh 1949). Barnes & Barnes (1965a) give a measurement of 192 μm long for a fully ripe egg (containing the stage I nauplius) of *A. modestus* from Pontevedra, Spain (42°25′), which is similar to that given by Crisp (1954) (93 μm wide × 190 μm long). The size of a Stage I nauplius at 125 × 250 μm (so a volume [*V*] of 2.05×10^{-6} mL) is larger than species of *Chthamalus* but smaller than *Semibalanus*, *Balanus* and *Tetraclita* species (see also Crisp 1987). It was suggested that a reduction in embryo, and hence naupliar, size might be associated with euryhaline behaviour, since those of *Amphibalanus improvisus* ($V = 1.26 \times 10^{-6}$ mL) had the smallest balanid embryo (Barnes & Barnes 1965a). However, the volume of the embryos of *Amphibalanus eburneus* ($V = 3.18 \times 10^{-6}$ mL) and *Austrominius modestus* are not that small, but this may be because although these two species are euryhaline, they are probably less so than *Amphibalanus improvisus*. In plankton samples from the Burnham-on-Crouch district, Knight-Jones & Waugh (1949) reported no appreciable difference in size between those liberated during the early and later parts of the season, but later stages were much more variable in size than earlier stages. Stage I nauplii of *Austrominius modestus* collected from the plankton in New Zealand measured 150 × 360 μm, while cultured stage I nauplii were smaller, measuring 100–110 × 210–230 μm (Barker 1976) or 120 × 250 μm (Foster 1967a,b). Please see Tables 6a and 6b for differences in the size of larvae cultured in Great Britain vs New Zealand. Stone (1988 and 1989) found differences in size of stage IV–VI nauplii reared using different diets (see her Figure 1, 1988, and Table III, 1989) (when temperature was 18 ± 0.2°C and a salinity of 35). Please see 'Physiology and Function' regarding laboratory experiments on the effects of salinity on the development of nauplii). Similar to Tighe-Ford et al. (1970), Harms (1986) noted that stage VI nauplii grew bigger at low temperatures and attained their maximum

Table 6a Size in μm of larvae of *Austrominius modestus*, acc. to Knight-Jones & Waugh (1949), based on laboratory and plankton samples (June–July 1948 from Burnham-on-Crouch district)

	Carapace		
Stage	Greatest width	Length	Total length
I	110–140	–	240–260
II	150–170	–	360–430
III	180–200	210–250	350–430
IV	220–250	290–350	390–500
V	260–310	340–440	450–570
VI	330–410	420–550	480–710
Cyprid	–	540–560	–

Note: Length and total length include the caudal spines.

Table 6b Size of larvae (µm) of *Austrominius modestus* reared by Barker (1976) and Foster (1967b), col. 4, 5 and 6 in New Zealand

	Carapace				
Stage	Width	Length**	Width	Length	Length/width
I	100–110	210–230	120	250	2.08
II	150–160	360–380	150	360	2.36
III	180–200	410–450			
IV	220–240	280–290**			
V	270–290	340–370**			
VI	350–370	440–480**			
Cyprid	230–260	510–580			

Note: Length** in stages IV, V and VI excludes the caudal spines and Foster (1967a,b) col. 4, 5 and 6.

size at a salinity of 30 (Helgoland). Nauplii from the two New Zealand populations sampled were smaller than those from Helgoland, with the smallest being those from adults from the relatively cool South Island site of Portobello (Harms 1986).

Occurrence in the plankton timing and distribution

Larval navigation

During the pelagic phase, the larvae of barnacles respond to various environmental variables (see e.g. Crisp 1974 for a description of barnacle and other marine invertebrate navigation). In Wellington Harbour, Port Nicholson, New Zealand, the aggregation of *Austrominius modestus* nauplii was positively correlated with water temperature but negatively with salinity (Cassie 1959a,b, 1960, 1962), while Martin & Foster (1986) found that the larvae of *A. modestus* were retained almost completely within Mahurangi Harbour in New Zealand. It was discovered that nauplii of *Austrominius modestus* in the photonegative condition can be made photopositive (resulting in them swimming upwards) after a positive change in hydrostatic pressure, but they do not respond to negative pulses or a fall in pressure (Knight-Jones & Qasim 1966). In northwest Europe, Crisp (1958) had shown how the rate of spread of *A. modestus* could be explained by relating the larval life in the plankton to eddy diffusion.

Timing of occurrence in the plankton in European waters

The timing and peaks in abundance of *Austrominius modestus* nauplii in the plankton varies with location, occurring throughout the year in some locations, but more seasonally in others. *Austrominius modestus* nauplii occurred in the plankton near Helgoland, Germany, from May to the end of October, but they were most abundant in July and August (Harms 1984). Further south, Lang (1980) mentioned the probable seasonal occurrence of nauplii of *A. modestus* in the plankton in Great Britain from April–November but questioned whether they are present in December–March. However, they have been found around the island of Anglesey, North Wales, throughout the year, but there were higher abundances in late summer and autumn (Bennell 1981). During weekly sampling in 1979–1981 of the plankton SW of the Isle of Man, Salman (1982) noted that the larvae of *A. modestus* were very rare. Further south, in Southampton water, plankton were sampled at fortnightly to monthly intervals at two stations, Calshot and Marchwood, in 1954–1959, as part of research on the impact of warmed water from Marchwood Power Station. During the summer, the plankton was dominated by barnacle larvae, especially those of *A. modestus* (Pannell et al. 1962). In the latter years of the study, there were higher numbers of *A. modestus* larvae, which they attributed to increased nutrient supply (run-off from the River Test) and a larger area for attachment (and hence more breeding stock) due to dock and port installations nearby. They also found that the higher densities also continued for a longer time into early autumn. As mentioned previously under 'Reproduction', the elevated temperatures may have allowed *Austrominius modestus* to extend its breeding season and hence supply of nauplii (Pannell et al. 1962). Burrows (1988) carried out plankton sampling in Plymouth Sound from June–September in 1983 (weekly–fortnightly) and 1984 (weekly). *A. modestus* nauplii were found throughout this time, but large numbers of stage VI nauplii only occurred from the end of July in 1983 and September 1984, which was reflected in settlement patterns on the shore. However, small numbers of stage VI nauplii occurred throughout the sampling period, which caused Burrows (1988) to suggest that larval release in *A. modestus*, in comparison to some other species of barnacle, may be induced by factors less obviously related to sea temperature. Ross et al. (2003) stated that *A. modestus* nauplii are common from May to October but can be found all year round. Similar to Burrows (1988), Ross et al. (2003) found large numbers of *A. modestus* nauplii in their samples from Plymouth, collected in July, August and September. Ross (2001) noted a clear differential distribution of the nauplii of *A. modestus* and other barnacle species in the plankton around Plymouth which mirrors the adults, but did not give any details. No significant differences in the abundance of stages II and III nauplii of *A. modestus* occurred between ebb and flood tide (Burrows 1988), which is similar to what Wolf (1973) had found for cyprids. Burrows (1988) also found that on certain dates, *A. modestus* nauplii were the least dispersed (and lost fewer larvae) of the barnacle species examined (contrasting sharply especially with the nauplii of the exposed coastal species *Chthamalus stellatus*), which is similar to what Martin & Foster (1986) had found in New Zealand in a semi-enclosed water body, like the Plymouth Sound. In the partially mixed Ria de Arousa (Galicia, NW Spain), *A. modestus* larvae were present in the estuary during the whole year, but there were variations in peak abundance between the sampling years (1999–2001) (Macho et al. 2010). Based on their sampling at seven stations within the estuary, *A. modestus* larvae were most abundant in the inner part, showing marked larval retention inside the estuary, reflecting adult distributions in the intertidal zone, similar to what had been seen by Ross (2001) in the Plymouth Sound.

Use of larvae for laboratory studies

Due to the availability of stage I nauplii in brooding adult *Austrominius modestus* throughout the year, at least in some locations in Great Britain, and the ease of rearing them to the cypris stage in the laboratory (Crisp 1957, Holland 1987), the cyprids of *A. modestus* have been used as test species in antifouling and biofouling tests, while the nauplii have been utilised to investigate the cycling of planktonic organic matter in marine food webs. Wisely (1960) refined some of the techniques to rear them in the laboratory in the winter months in Great Britain, while Neal et al. (1986) examined how lipid changed when the faecal pellets of *A. modestus* nauplii were 'repackaged' into bigger pellets during coprophagous feeding by adult *Calanus helgolandicus*. Not only were characteristic algal hydrocarbons totally removed during feeding by the *A. modestus* nauplii, but also most of the dietary polyunsaturated fatty acids, but changes to dietary sterols were less marked. They suggested that such 'repackaging' during coprophagy may result in a higher direct input of C_{28}–C_{29} sterols to marine sediments than herbivory. Vay et al. (2001) examined digestive enzyme levels during development in the larvae of *A. modestus*.

Cyprids

Description and identification

A combination of carapace shape, pigmentation and relative size can be used to distinguish *Austrominius modestus* cyprids from those of other barnacle species occurring in European (e.g. Knight-Jones & Waugh 1949, O'Riordan et al. 2001) and Australasian (Barker 1976) waters. The cyprids of *A. modestus* are colourless to a pale straw colour and of glassy transparency (Knight-Jones & Waugh 1949, Norris & Crisp 1953). Following the work of Knight-Jones & Waugh (1949), Norris & Crisp (1953), Barker (1976) and Tighe-Ford (1977), O'Riordan et al. (2001) summarised the diagnostic carapace shape of the cyprid of *Austrominius modestus* as elongated, with a *sharp angle between dorsal and ventral surface at anterior end*; posterodorsal margin rises steeply to an angle then evenly curved; narrowly curved posterior end. The carapace is dorso-ventrally compressed, and it has a fusiform shape (Barker 1976, p. 145 and 6, Tables 2 and 3 therein). Al-Yahya (1991) reared the cyprids of *Austrominius modestus* and other species of barnacle in the laboratory (at 20 ± 2°C) and described their comparative external morphology. He provided some of the most detailed descriptions of the whole cyprids and key features, using scanning electron microscopy (see his Plates 4.20 and 4.22), as well as dimensions. The SEMs include the antennular attachment disc and organs which the cyprids use to selectively explore a surface before attachment and settlement (see subsequently). See also Jensen et al. (1994a,b) and Moyse et al. (1995) for more SEM studies of the cyprids, and Elfimov (1995) regarding the cyprid carapace. Tables 4.1 and 4.2, Figures 4.3 and 4.4 and Plates 4.20 and 4.22 of Al-Yahya (1991) are invaluable to distinguish the cyprids of nine species of barnacle that occur in the waters around Great Britain, while O'Riordan et al. (2001) tabulated (Table 1 therein, p. 310) those of cyprids of intertidal barnacles in European waters. The position of the eyes appears to vary according to the degree of extension of the antennules (Barker 1976).

Cyprid size in the plankton and laboratory cultured

Cyprids of *Austrominius modestus* collected in the wild or cultured under different conditions in the laboratory vary to some extent in length and width. Having reared the cyprids of six species of New Zealand barnacle in the laboratory, Barker (1976) flagged that size alone is an unreliable character to distinguish cyprids of different species, due to great variation, even when cultured in identical conditions, and those from the plankton are often larger. Some of the differences in the size range of cyprids seen in the wild are due to the effect of adult barnacle size on the size of ova and embryos, which then follows through to naupliar and cyprid size (Barnes & Barnes 1965b).

Cyprids of *A. modestus* collected from the intertidal at Roscoff, NW France, in late summer 1997 and 1998, which were distinguished from the cyprids of other species by their carapace shape, measured between 450 and 625 μm in length (O'Riordan et al. 2001). Those collected by Wolf (1973) from the plankton in the Dutch Wadden Sea in May 1967 were towards the smaller size, with a mean length of 444 ± 15 μm by 216 ± 11 μm ($n = 100$), while those from September 1967 measured 450 ± 16 μm by 217 ± 11 μm ($n = 40$). Cyprids collected from the plankton in the River Crouch, Essex, southern England, were larger (540–560 μm), and only showed a 20 μm variation in length, but others from the east coast of England varied between 500 and 600 μm (Jones & Crisp 1954 cited in Wolf 1973).

Cyprids cultured in the laboratory in Great Britain varied in size depending on the temperatures at which that had been reared as well as the location from where the adults had been collected. Those reared by Al-Yahya (1991) measured 467–552 μm by 191–247 μm, with a L/H ratio of 2.33, while cyprids reared in Wales, for SEM studies, ranged in length from 470–550 μm, with a mean of 510 μm (Moyse et al. 1995). Cyprids were larger when reared at 10°C (535–646 μm by 212–273 μm; mean 587 and 245 μm) than at 20°C (515–576 μm by 232–273 μm; mean 545 and 254.5 μm) (Tighe-Ford et al. 1970) or varied from a mean of 472.2–562.0 μm by 221.5–277.8 μm (Tighe-Ford 1977), while those reared in New Zealand by Barker (1976) at 20°C measured 510–580 μm by 230–260 μm. On average, cyprids of *A. modestus* are about 100 μm smaller than those of than those of *Perforatus perforatus* (Mean length 698 ± 53.2 μm) (Norris & Crisp 1953).

Length of time to development to the cypris stage and effects of different diets and temperatures

Similar to the nauplii, the rate of development to the cypris stage is affected by different diets, temperatures and light conditions. Moyse (1960) described how to successfully culture *Austrominius* *modestus* cyprids in the laboratory. He reared stage I nauplii taken from the mantle cavities of adult *A. modestus* to cyprids in six days at 22°C and in any month of the year, which is much shorter than the time it takes for the cyprids of *Semibalanus balanoides* or '*Chthamalus stellatus*' to develop. Comparing the success rate and length of time to the cypris stage of *Austrominius modestus*, using different species and densities of flagellates and diatoms, cyprids were obtained within five days, using a unialgal diet of the diatom *Skeletonema costatum* (Moyse 1963). These cyprids successfully settled, metamorphosed and grew to adult size (8 mm) on the same diet, while it took ten days and fewer cyprids were produced when fed the diatom *Phaeodactylum closterium*. It took Walker (1973) slightly longer (seven to nine days) to rear cyprids of *Austrominius modestus* from Stage I nauplii taken from the mantle cavities of adults in at 20°C, while it took Al-Yahya (1991) seven days.

Wisely (1960) investigated the effect of a number of different temperatures and flow rates, but used *Phaeodactylum tricornutum* supplemented with dried liver powder, and obtained over 3000 settling cyprids, with the first cyprids appearing after 15 days. Nauplii and cyprids were reared at the same temperature using *Skeletonema costatum* (Tighe-Ford 1977), but juvenile hormone analogues affected the size of the cyprids (see details previously in 'Physiology and function'). In the laboratory, larger cyprids of *A. modestus* were produced at lower temperatures, but they took longer to develop (21 to 34 days at 10°C vs 11 to 17 days at 20°C, with a diet of *Skeletonema costatum*), but cyprids were obtained after six days at 20°C (Tighe-Ford et al. 1970). Barker (1976) collected adults from the Leigh area, Auckland, New Zealand, used *S. costatum* to rear *Austrominius modestus* and tried three different temperatures (20, 25 and 30°C) but only got cyprids at 20°C and after six days. Tighe-Ford et al. (1970) agreed with Moyse (1963) that food was a critical factor for fast rearing of the cyprids. At 16°C, the cyprids could be obtained after 12 days when there was constant light, but it took 17 days in the dark, which might have been due to greater availability of food in the former conditions, whereby the diatoms could multiply (Tighe-Ford et al. 1970). Mortlock et al. (1984) determined the effects of farnesol on the last stage nauplii and cyprids of *A. modestus*. Metamorphosis of nauplii to cyprids and then to adults was accelerated at farnesol concentrations of 1 ppm. Finally, it was observed that in laboratory conditions when kept in shallow dishes, the cyprids of *A. modestus* may become trapped in the surface film, which was suggested to be due to the cuticle of the cyprid being strongly hydrophobic (Knight-Jones 1953).

Cyprids in the plankton

Although non-feeding (instead they use their stored lipid globules), barnacle cyprids are highly active, swimming for up to several weeks (Crisp 1974). As mentioned previously with respect to the nauplii, the authors are unaware whether any researchers have calculated how long the relatively small cyprids of *Austrominius modestus* can survive in the water column, but there are some published data on where and when they occur in the plankton. In the Wadden Sea, *Austrominius modestus* cyprids showed a groupwise occurrence at sampling depth, but this grouping appeared to be independent of the tide, but the need for more data was pointed out (Wolf 1973). No significant correlations in numbers of cyprids of *A. modestus* were found with chlorinity, silt, sand, total suspended matter or current velocity, which was very different behaviour to the cyprids of two other species studied (*Amphibalanus improvisus* and *Balanus crenatus*) (see Figure 8, p. 30, and Table XII, p. 31, of Wolf 1973). There was only a slight association of the cyprids with warm water, which suggested that they may have a slightly lower density than the seawater, which could affect their distribution in the water column (Wolf 1973). As mentioned previously, this is different to what Cassie (1959a,b, 1960, 1962) had found for stage V and VI naupliar stages of *A. modestus* in New Zealand, but this could be due different larval stages showing different behaviours. Unfortunately, Wolf (1973) did not separate VI stage nauplii into species of barnacles, but he identified cyprids of *A. modestus* in samples collected in May 1967, September 1967 and September 1969, but no *A. modestus* cyprids were recorded in the July 1967 sample. On shores studied in Plymouth, the cyprids of *A. modestus* occurred around the same time as those of *Chthamalus montagui* and *C. stellatus* in 2002 and 2003, and although their size overlapped, they could be distinguished clearly (Jenkins 2005).

Settlement and recruitment

Settlement

The moment when a planktonic larva attaches to a substrate can be defined as settlement (Keough & Downes 1982). Given the sessile nature of metamorphosed barnacles, the settlement location is very important; however, the point of attachment on a substrate is not entirely fixed, and barnacles can exhibit limited mobility (up to a few times their own diameter) when subjected to lateral pressure (Crisp 1960a). Barnacle larvae can settle on a variety of surfaces, but cyprids exhibit a preference for settling in grooves or depressions (Crisp & Barnes 1954). Using *Semibalanus balanoides* as their model organism, Hills & Thomason (1996), carried out some of the most detailed research on settlement surfaces, not just their type, but also roughness, texture ISO, contour and so on and created a 'Potential Settling Sites' index. *Semibalanus balanoides* settlement was found to be higher on rough as opposed to smooth surfaces (Hills & Thomason 1998).

Hills & Thomason (1996) outlined two processes controlling barnacle settlement. The first is oceanic currents, which transport barnacle larvae and control the locality where a cypris larva will settle. As long as the cyprids are physiologically ready to settle (Whillis et al. 1990), once present in this locality, the cypris larva will locate a suitable substrate, which is the second controlling factor, to settle on. Cyprids possess antennules, with many sensory organs. The cyprid carries out an exploratory walk (see e.g. Knight-Jones & Crisp 1953), attaching itself to the substrate at various locations via the antennules, presumably to test the adhesive nature of the surface (Crisp 1985), and leaving behind footprints of adhesive material, which may be used as settlement cues for other cyprids (Moyse & Knight-Jones 1967, Crisp 1974, 1985). The cypris larvae investigate the substrate from a broad scale to fine scale, with increasing attention given to substrates approaching the point of final attachment (Rainbow 1984).

Barnacles exhibit gregarious settlement, with cyprids readily settling where adult barnacles already exist. *Austrominius modestus* was the first barnacle species in which this was demonstrated (Knight-Jones & Stevenson 1950). This adaptation is advantageous, as their presence indicates a low risk of early mortality and thus a suitable habitat for survival; however, the tendency to settle close to adults of the same species should be stronger than different barnacle species, given the importance of cross-fertilisation and reproductive success (Patel & Crisp 1961, Moyse & Knight-Jones 1967, Crisp 1990). This is particularly important in species which are obligatory cross-fertilisers, such as *A. modestus*, which, as mentioned in 'Reproduction', requires another individual to settle within ~5 cm to allow copulation and fertilisation. The need for enough individuals to settle near one another to allow copulation was termed the 'critical breeding density' by Crisp (1958) and is one of the factors that slowed the speed of the spread of *A. modestus* in Europe.

Barnacles have the ability to distinguish between individuals of the same species or different species during settlement (e.g. Barnett & Crisp 1979, Barnett et al. 1979, Moyse & Hui 1981, Crisp 1990). Arthropodin, which is the settling factor responsible for elucidating gregarious settlement responses, is found in high concentrations in the integument of arthropods and is especially abundant in animals with recently formed cuticles, such as a newly settled barnacle or one which has just moulted (Crisp & Meadows 1962). It is possible that the very high moulting rate that occurs shortly after the release of larvae (which follows a long intermoult period when brooding embryos (see 'Reproduction' section)) promotes the settlement of other larvae in the water column at this time. No evidence of chemotaxis to arthropodin was found in barnacle cyprids when they are in the water column, since it was only when they alighted on treated surfaces that the cyprids showed a response.

Settlement of Austrominius modestus in response to its own and other species

In field experiments, settlement of *Austrominius modestus* is much higher on glass slides bearing *A. modestus* than on bare glass slides and on glass and slates plates placed in shelly areas, where barnacles are numerous, than those deployed in muddy areas where barnacles are absent. However, occasional individuals will settle in areas where settlement is sparse, which allows the colonization of new areas, and gradually other individuals will settle near these pioneers (Knight-Jones & Stevenson 1950). The gregarious behaviour not only facilitates reproduction, but also brings cyprids to habitats where other individuals have survived, thus reducing wastage through individuals settling in unsuitable localities and in isolation (Knight-Jones 1953). Cyprids respond more to the arthropodin of their own species, but that of related species evokes a similar, but less effective, response (Crisp & Meadows 1962). For both *A. modestus* and *Semibalanus balanoides*, lower concentrations of extracts (Crisp & Meadows 1962), or the presence of the same species of adult on stones (Knight-Jones 1955), induced higher settlement of its own species in comparison to the extract/presence of the other. Extracts of *'Chthamalus stellatus*' induced some settlement of *Semibalanus balanoides*, but was less effective than extracts of *S. balanoides*, *Balanus balanus* or *Austrominius modestus* in descending order of effectiveness (Crisp & Meadows 1962). *Balanus crenatus* also caused settlement of *Semibalanus balanoides* (Knight-Jones 1955). Similarly, Larman & Gabbott (1975) found that *Austrominius modestus* cyprids readily settled on slates treated with extracts of both *Semibalanus balanoides* and *A. modestus,* while *S. balanoides* cyprids showed a preference for slates treated with *S. balanoides* extracts. Whillis et al. (1990) noted that there was little evidence for a graded systematic response to allospecific arthropodins, with *Chthamalus montagui* showing twice as much settlement in response to conspecific proteins, but no significant difference between the arthropodins of *A. modestus* and *Semibalanus balanoides.* The cyprids of *Austrominius modestus* often settle in close proximity to adult barnacles, both *A. modestus* adults and other barnacle species (Hui & Moyse 1982). Since *Austrominius modestus* is less discriminating than, for example, *Semibalanus balanoides*, as demonstrated by the fact that *A. modestus* cyprids can be induced to settle in response to ovalbumin, but not *S. balanoides* or *Balanus crenatus* (Larman & Gabbott 1975), it will settle in areas which are colonized already by other species and hence facilitate its spread, while Moyse & Hui (1981) noted that it may be adaptive, at least in some situations, for *Semibalanus balanoides* cyprids to settle near *Austrominius modestus* spat or adults, rather than conspecifics, since *S. balanoides* can outcompete *A. modestus* for space (Crisp 1964a,b).

Gregariousness and spacing: Although the cyprids of *Austrominius modestus* are gregarious during settlement (e.g. Knight-Jones & Stevenson 1950, Knight-Jones & Crisp 1953, Anger 1978), they may space themselves out during settlement (e.g. Crisp 1961, Knight-Jones & Moyse 1961, Moyse & Hui 1981), seeking bare spaces (Connell 1961a) and rarely touch their own species (Knight-Jones & Moyse 1961), including other recently settled *A. modestus* spat (Hui & Moyse 1982). However, Barnett et al. (1979) and Barnett & Crisp (1979) had reported that they were gregarious even at very close range, but Moyse & Hui (1981) pointed out problems with their experiments and conclusions. Hui & Moyse (1982) examined *A. modestus*'s settlement near spat of four different sizes, as well as adults of five different lengths. They found that territorial spacing occurs when the established individual is below 2 mm long. Settlement in the 'straddling' position is common when the established individual is over >3 mm long, whilst there is a combination for the 2–3 mm category. Furthermore, larger sizes (above 2.5 mm) were found to be increasingly attractive, for example, with 0.695 spat per adult in the >4 but <5 mm category, versus only 0.093 in the >2.5 but <3 mm (see Table 3 and Figure 1 therein).

Moyse & Knight-Jones (1967) reported that both *Semibalanus balanoides* and *Austrominius modestus* tend to space themselves out during settlement. They suggested that the short generation time of *A. modestus* reduces the chance of new recruits being able to reproduce before being crushed or lifted off by the adults. The reason for maintaining distance between *A. modestus* spat is that they offer no mechanical protection, suffer high mortality and grow quickly, posing a competitive threat (Hui & Moyse 1982). This spacing out prevents overcrowding and smothering (Knight-Jones 1951, Knight-Jones & Moyse 1961). Furthermore, this behaviour during settlement may be a factor contributing to the spread of *A. modestus*, as individuals which do not settle within dense aggregations of their own species will not necessarily be at a disadvantage (Larman & Gabbott 1975), provided there are other *A. modestus* individuals in close enough proximity to facilitate cross-fertilisation. When there is dense settlement and rapid growth, *A. modestus* may form hummocks, within 8 to 10 weeks of settling, but more settlement can still occur between and on top of the existing barnacles in the hummock (Luckens 1975). Leslie (1968) noted that on New Zealand shores, *A. modestus* has a tendency to occur in clusters.

Effect of substrate type on settlement of Austrominius modestus

Austrominius modestus is able to settle on a wider range of substrates, both natural and man-made, than some other barnacle species. It has been suggested that for *A. modestus*, the type of substrate is immaterial if conditions are otherwise suitable (Moore 1944). In its native range, *A. modestus* had been recorded on rock, concrete, iron and wood, in addition to living plants, algae, cirripedes, bivalves, gastropods, crabs, loricates and ascidians, as well as a brachiopods (Moore 1944, Luckens 1975). Zauke et al. (1992) added gravel and lava to this list of substrates for adults collected in Auckland, New Zealand. In its introduced range, *A. modestus* has been recorded similarly on numerous types of substrates, including on gastropod molluscs, crabs, tunicates, flotsam and jetsam (Hartog 1953), such as plastic litter in the Shetland Islands (Barnes & Milner 2005), as well as on *Semibalanus balanoides* and its own species. *Austrominius modestus* (and *Balanus crenatus*) were found on intertidal peat beds on the beach of Raversijde, Belgium (Jocqué & Van Damme 1971). *Austrominius modestus* does show some preferences, since where contiguous wood and iron surfaces were available, the wood was colonized much the faster (Moore 1944). Kathiresan & Bingham (2001) commented that some species of Subfamily Elminiinae appear to prefer mangroves over other substrates in South Australia, with *A. modestus* being recorded on the pneumatophores of the white mangrove tree *Avicennia marina* (Womersley & Edmonds 1958, Hutchings & Recher 1982, Bayliss 1982). In Cork Harbour, Ireland, a few *Austrominius modestus* individuals were recorded fouling on the test of another introduced species, the Korean sea squirt *Styela clava* (K. Swain & A. Greer, pers. obs. in May 2019), although Moore (1944) noted that *Austrominius modestus* favours moving, as opposed to sessile, animals as hosts. *Austrominius modestus* occurs on oysters and mussels in New Zealand (e.g. Ralph & Hurley 1952, Foster 1978) as seen in Ireland, too. In turn, *A. modestus* may itself form a suitable substrate, and in New Zealand, *A. modestus* is one of the substrata on which the barnacle *Chamæsipho columna* may occur (Moore 1944).

A number of types of substrate have been deployed as settlement panels for *Austrominius modestus*. The readiness of *Austrominius modestus* to settle (and stay attached) on glass plates was used to study its gregarious settling and brooding (Knight-Jones & Stevenson 1950, Crisp & Davies 1955). More cyprids were lost from smooth glass than frosted, suggesting a benefit of indentations, albeit small, for cyprid attachment and subsequent survival (Knight-Jones & Stevenson 1950). Crisp & Barnes (1954) labelled this tactile response rugotropic. In the summers of 1947–1949, in Burnham-on-Crouch, Great Britain, smooth slate plates that had been deployed to monitor oyster spat recruitment were usually covered by *A. modestus* within a few days (Knight-Jones 1948). When settlement was low, the cyprids tended to settle first in groups, but when it was very heavy, they noted that their distribution on these smooth plates was remarkably even. Demonstrating their rugophilic response, they noted that *Austrominius modestus* settled particularly abundantly in scratches and when there were surface irregularities. For *A. modestus*, slate panels were used also by Crisp &

Meadows (1962), while others tried roughened perspex (O'Riordan, unpublished), plexiglass (Anger 1978, Harms & Anger 1989) or Bakelite (Crisp & Barnes 1954).

Effects of biofilms on Austrominius modestus

Not only the surface itself and the presence/trace of other barnacles may be important to induce *Austrominius modestus* to settle, but also other organisms. Biofilms have both an inhibitory and stimulatory effect on *A. modestus* settlement (Hills & Thomason 1996), which is dependent on biofilm age (Neal & Yule 1994a,b). Relatively thin, dense multispecies biofilms associated with a high shear regime (83 s^{-1}) gave increased tenacity by *A. modestus* (and *Perforatus perforatus*) cyprids in comparison to relatively thick, less dense biofilms associated with a low shear regime (15 s^{-1}) (Neal & Yule 1994a,b). Although tenacity was significantly greatest for high-shear films for both species, *Austrominius modestus* cyprids attached as strongly to low-shear films as they did to unfilmed surfaces, but *Perforatus perforatus* showed better attachment to the latter. Differences between the two barnacle species towards the same biofilm suggested that differential settlement may play a more substantial role in the distribution and zonation than does post-settlement mortality (Neal & Yule 1994a,b). Furthermore, *A. modestus* showed a preference for long-immersed surfaces (see Table 4 in Skerman 1958), especially those with *A. modestus* already present. Panels which had been immersed only one month had a maximum of 26 *Austrominius modestus* per 100 cm^2 versus over 900 per 100 cm^2 on one that had been immersed two months.

Orientation of Austrominius modestus to light

Austrominius modestus orientates to light at settlement, and no rotation occurs during metamorphosis (Barnes et al. 1951). Although in deep grooves this orientation may be a response to light, in shallow grooves it is due to a rugophilic response (Barnes et al. 1951). Cyprids of *A. modestus* were found to prefer to settle on the illuminated upper side of horizontal opaque panels, being photopositive but geonegative at settlement, while *Semibalanus balanoides* settled preferentially on the undersides (Crisp & Ritz 1973). Crisp & Ritz (1973) noted that previously Barnes et al. (1951) had found higher settlement of *Austrominius modestus* on the lower surface of a horizontally exposed panel, but Crisp noted that he and his co-authors at that time had not monitored the light intensity on either side of the panel. When the numbers of spat and adults of four barnacle species, including *A. modestus*, were monitored on south- and north-facing surfaces at eight different heights above chart datum in Warwick Bay, Dale, Pembrokeshire, the zonation of the *A. modestus* spat agreed with those of the adults, with highest densities of spat and adults at 2.7 m above CD, but densities of both were lower on north-facing surfaces (adults: 50 per 100 cm^2 vs 300 per 100 cm^2; spat: 10 per 100 cm^2 vs 100 per 100 cm^2) (Moyse & Knight-Jones 1967).

Although barnacle cyprids are known to be selective in their settlement, they cannot delay settlement indefinitely and become less discriminative with age and in extreme cases may lose their ability to metamorphose (see e.g. Knight-Jones 1953).

Timing and level of settlement

The timing and abundance of settlement vary with location. In Australasia, in its native range, juveniles were found to be plentiful always (Moore 1944), with settlement occurring at any time of year in Auckland, both intertidally and subtidally (Luckens 1975). Elsewhere, in New Zealand, at Queen's Wharf, Port Nicholson, Wellington, settlement of *Austrominius modestus* was monitored on subtidal (1.2 m below low-tide level) Oregon pine test blocks (Ralph & Hurley 1952). Those which were deployed just for a single month showed settlement with a density of $\sim$4 cm^{-2} in May, the month of highest settlement. On long-term blocks, deployed for 13 months, only a few *A. modestus* were found, which was attributed to a failure to survive. *Austrominius modestus* was moderately common in May, July, October and November, but only rare in April, suggesting that the temperature may not have been an important factor (Ralph & Hurley 1952). Other fouling species (but not any other barnacle species) persisted on the blocks during this time, although no single species became dominant. At the same site, *A. modestus* was recorded also on wharf-piles and the mussel *Mytilus planulatus* (Ralph & Hurley 1952). At Lyttleton, South Island, New Zealand, settlement occurred on subtidal plates from March–November (none from December–February), but the peak settlement, in autumn and spring, was thought to be related to seasonal abundances of food for the plankton (Skerman 1958). However, cyprids were found enmeshed in polyzoan colonies in January and February, which, although not identified in the laboratory, were thought to be *Austrominius modestus*. The austral summer high temperatures during January and February were not thought to have restricted spawning or larval development, since *A. modestus* settles prolifically during these months in Auckland Harbour, where summer temperatures are an average 3°C to 4°C higher than Lyttelton (Skerman 1958). Instead, other species attached to the panels, for example, the polyzoan *Bugula* sp., may have competitively depleted the settlement and affected the growth rate of *Austrominius modestus* in certain months, either by drastically reducing the food supply in their vicinity or by mechanically fouling their opercular plates (Skerman 1958).

In its introduced range, *A. modestus* has been described as having a remarkably long settlement season (Knight-Jones & Waugh 1949), lasting longer than some of the native species (e.g. see Figure 4 for a comparison of the timing of settlement of *Semibalanus balanoides*, *A. modestus* and *Chthamalus montagui* at sites in SW Ireland in 2014 and 2015). This provides it with an increased likelihood of encountering free substrate suitable for settlement. However, this trait is not always advantageous, since high densities of *Austrominius modestus* can produce small individuals with slow growth and maturation rates. In Great Britain, the native species *Semibalanus balanoides*, which occupies a similar part of the intertidal zone as *Austrominius modestus*, settles approximately one month prior to the peak of *A. modestus* settlement, allowing the native species to utilise any substrate made available during the winter months (Crisp & Davies 1955). However, it has been suggested that *A. modestus* exhibits adaptations which compensate for a later settlement than *Semibalanus balanoides* (usually in April and May, when there is plenty of bare space) (Harms 1984, citing Lewis 1964). These adaptations include settling for a longer period; for example, in Helgoland, Germany, *Austrominius modestus* settlement (sum of individuals settled on panels during the subsequent one-month period) takes place from June to October (Harms & Anger 1983) at higher shore levels than *Semibalanus balanoides* (Kühl 1954), as well as subtidally from June to October and March–April (Anger 1978, Harms & Anger 1983, 1989). At many locations on the German coast, settlement was found to occur from May–June to October–November (Kühl 1963). In Den Helder, in the Dutch Wadden Sea, *Austrominius modestus* settlement begins in May and continues until late in the year (Wolf 1973), which, according to Wolf (1973) is similar to that recorded in Portsmouth, in southern England (Houghton & Stubbings 1963), and on the east coast of England (Knight-Jones & Waugh 1949). On shores where they co-occur and where there is no modifying effect of wave action, *A. modestus* can survive 30–60 cm higher than *Semibalanus balanoides*, which is probably dependent on the chance occurrence of favourable conditions during emersion (Foster 1971a,b). A longer settlement season gives *Austrominius modestus* a greater chance than *Semibalanus balanoides* of settling, growing and surviving high on the shore (Foster 1971a,b). In a ten-year study, the settling intensity and settling success of *Austrominius modestus* varied between years, with lower levels in springs following unusually cold winters, when adult populations in the German Bight were decimated (Harms & Anger 1989). On subtidal panels, barnacles (*A. modestus* and *Balanus crenatus*) covered up to 70%–100% of the surface at the end of the season (Harms & Anger 1989). During their surveys monitoring the spread and changes in abundance of *Austrominius modestus* on the continental coast in 1963, Barnes & Barnes (1965b, 1966) noted if spat were present: in France, they found them on 15th June

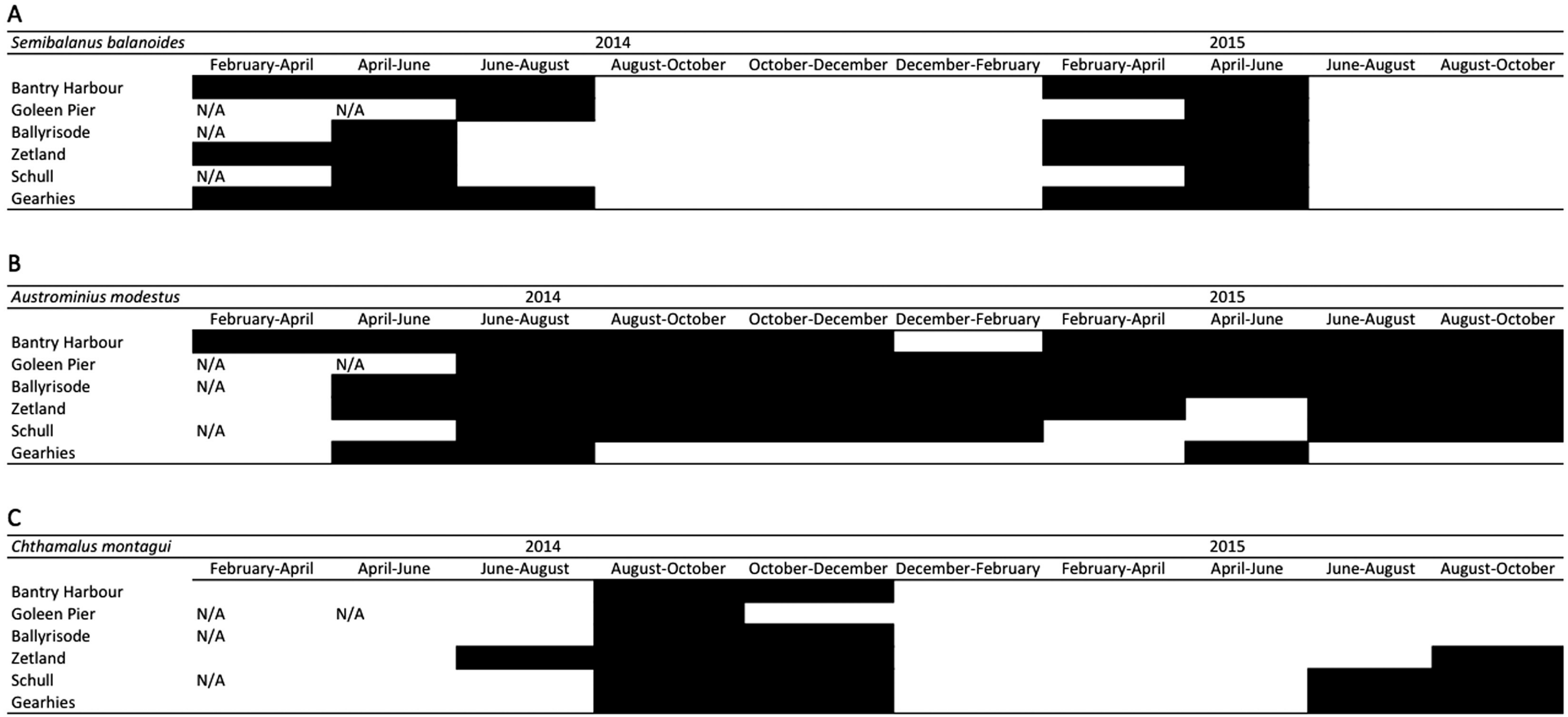

Figure 4 Timing of settlement of *S. balanoides*, *A. modestus* and *C. montagui* at sites in SW Ireland in 2014 and 2015.

at Pornic, in the Arcachon Basin at La Pointe Lavergne and on pignots in the upper part of the Chenal du Gujan and in Spain at Villaviciosa (30th June) and at Costa Nova do Prado, Portugal, on 11th July 1963.

Variation in the length of the settlement season with latitude in its introduced range: There are differences in the length of the settlement season of *Austrominius modestus* with latitude, with shorter seasons further north. For example, in Scotland, settlement was negligible on sites on the west coast except during the summer (Barnes & Barnes 1962), while on test panels immersed at Rosyth, in 1960, it occurred in late summer–early autumn (August, September and October) (Hemingway-Jones 1961). Further south, at Menai Bridge, North Wales, it was suggested that it was mostly in the summer months (May–September), with main peaks in June–July, but none was detected during winter (December–March) (Wisely 1960), but another author proposed that season did not restrict settlement of *A. modestus* there (Foster 1971b). At Menai Bridge, *A. modestus* could settle much higher than *Semibalanus balanoides*, with, in April 1968, the extreme highest specimens of *Austrominius modestus* occurring 40 cm above those of *S. balanoides* on a sheltered shore (Foster 1971b). In the Menai Straits, Anglesey, on transects that were monitored from 1974–1979, fluctuations in *Austrominius modestus* were recorded, with peaks of *A. modestus* abundance occurring when that of *Semibalanus balanoides* were relatively low (Bennell 1981). Although the cyprids of *Austrominius modestus* could be found in the plankton and on the shore at most times of year, the numbers were much less than the latter species. The timing of the peak of settlement of *A. modestus* varied greatly between years, with juveniles being most abundant from July to September in four years of the study but between October to December in two other years (1975 and 1977) (Bennell 1981). In south-east England, a similar season was seen as in North Wales, but the settlement was lighter there (Wisely 1960). In Burnham-on-Crouch, in 1948, settlement of *A. modestus* and *Amphibalanus improvisus* occurred with varying intensity from May to September but with most settling during this period being *Austrominius modestus* (Knight-Jones & Waugh 1949). The onset of settlement was thought to be related to a low sea water temperature of 14–15°C (Stubbings & Houghton 1964). In Chichester Harbour, which was described as muddy, with a high salinity, with little freshwater influx, *A. modestus* settled on subtidal panels (at a depth of 60–90 cm) from May to October between 1945–1949, but peak settlement was between June and September. In 1955, low levels of settlement were recorded also in late November/early December (seawater temperature was 7.2–8.3°C) (Stubbings & Houghton 1964). On weekly collected panels, between 1950 and 1955, settlement lasted between 16 and 22 weeks, with two peaks of settlement, a month to six weeks apart, in some years, while in other years, there just seemed to be one (Stubbings & Houghton 1964).

The number of settlers

The number of *Austrominius modestus* settlers can vary with time of year, location, depth, length of deployment and substrate. In Helgoland harbour, a maximum of 0.73 cm^{-2} were recorded on one-month subtidal panels in late August–September (Anger 1978). In Chichester Harbour, west Sussex, Great Britain, an average settlement of 31 cm^{-2} was seen in July 1945 on subtidal (60–120 cm deep) Bakelite panels, eight times higher than that seen at Wellington, New Zealand, on panels deployed at a similar depth (Ralph & Hurley 1952). Stubbings & Houghton (1964) recorded a total annual settlement varying from 10 919 to 140 891 (see Table 9 therein). The maximum settlement of *A. modestus* on one of the subtidal panels was 20 cm^{-2}. In 1952, in Brixham Harbour, South Devon, settlement was 0.01 cm^{-1} (Crisp & Davies 1955), but up to 50–100 cm^{-1} of spat could be recorded after just a week in June and July in the River Crouch in Essex. In Essex also, Waugh (1957) recorded up to 230 cm^{-2} on smooth slates. In southern Ireland, at Lough Hyne Marine Nature Reserve (LHMNR) (Ireland's only marine nature reserve), Lawson et al. (2004) found that intertidal settlement of *A. modestus* was highest from April–May and August–September, with settlement being over 300 times higher than that of *Semibalanus balanoides.* One of the reasons for its success there is the high water retention levels within the lough, as well as elevated temperatures in comparison to outside the lough, which may allow higher reproduction and retention of larvae. Gallagher et al. (2017) reported that although *Austrominius modestus* is the dominant barnacle in the intertidal at LHMNR, native barnacle species still co-exist with it there. Please see Watson et al. (2005) subsequently regarding intertidal and subtidal barnacle recruitment and survival at the Lough.

Post-settlement factors

Usually, barnacle settlement occurs over a much broader area than that eventually occupied by adults, as there are a variety of factors influencing the settled larvae or spat post settlement. In addition to these post-settlement factors, some species display zonation within the plankton, which may influence location of settlement, and patterns of zonation on the shore (Grosberg 1982). The availability of space for settlement is the factor which ultimately controls population size (Crisp 1960a). Settlement success can be determined by competitive interactions; initially, there is competition between larvae for suitable attachment substrates, and following this, developing juveniles are subject to competition from neighbouring barnacles (Svensson et al. 2006).

Based on his finding of very large specimens of *Austrominius modestus* in a drowned river valley with very strong tidal currents in northern France, Bishop (1954) suggested that the most advantageous site for barnacles to settle are those where the water movement is as great as they can tolerate. However, with respect to wave-exposed shores, Crisp (1958) suggested that cyprids of *A. modestus* do not settle there, rather than settling and then suffering post-settlement mortality due to wave action (but see previously regarding their shell structure) or predation. It was noted that since mortality of the cyprids and young adult stages of *Semibalanus balanoides*, *Austrominius modestus* and especially *Balanus crenatus* occurs naturally and regularly during intertidal emersion in dry weather, colonization of higher shore levels by these species depends on the coincidence of settlement with a sustained period of humid conditions of emersion (Foster 1971a). Maybe this is the same for *Austrominius modestus* in the hot, dry conditions of southern Portugal, its currently recorded southern introduced limit. It would be interesting to examine whether there is any difference in the rates of settlement of cyprids, successful metamorphosis and recruitment of *A. modestus* and native species at different latitudes in its introduced range, including whether there are any differences in success with day versus night attachment, as was done for chthamalid cyprids (Cruz et al. 2005).

Despite the profound structural reorganisation that is involved, barnacle cyprids require in general less than 24 hours to metamorphose into the metamorph (Crisp 1974). Under laboratory conditions, it has been reported that the cyprid *A. modestus* can metamorphose in a much shorter time, from less than four (Knight-Jones 1953, Knight-Jones & Crisp 1953) to eight (Crisp 1974) hours, although Tighe-Ford et al. (1970) noted that it occurred normally within three days. Walker (1970) had described the cement apparatus used to attach to the substrate of *A. modestus*, along with the cement apparatus of two other species of barnacle.

Recruitment

Recruitment has been defined as the number of individuals surviving for a certain amount of time, in the case of barnacles usually 30 days following settlement (Jenkins 2005). The ability of a species to colonize an area can be estimated by measuring its recruitment rate over a certain time period (Keough & Downes 1982), and panels and areas of cleared rock have been used by various authors to examine barnacle recruitment. The recruitment of *Austrominius modestus* was examined on artificial structures in cleared areas ranging in size from 6 to 25 cm^2 (Bracewell et al. 2013). Higher recruitment was seen in the larger plots, increasing until a maximum density was reached, after which there was a decline in settlement. This study confirmed that *A. modestus* has the ability to

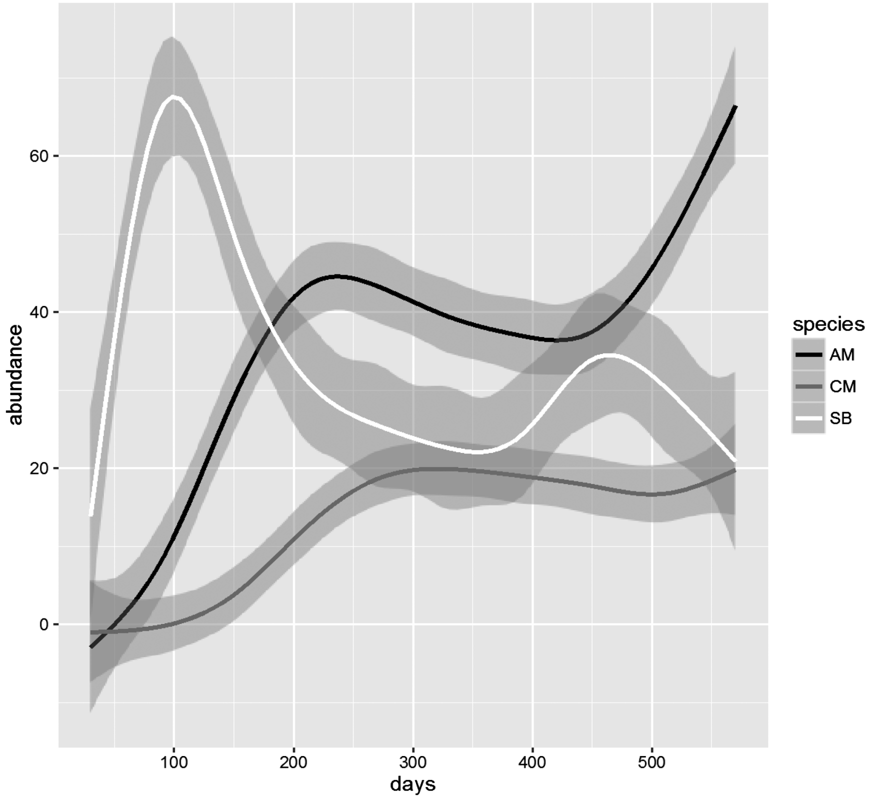

Figure 5 Number of recruits in clearance plots over an 18-month period – numbers are an average for all field sites and all shore heights sampled in south-west Ireland. AM, *A. modestus*, CM, *C. montagui*, SB, *S. balanoides*.

rapidly colonize free space made available, in this case in the form of an artificial substrate (see also Bracewell et al. 2012).

As mentioned previously, barnacle larvae are known to show a preference for rough as opposed to smooth surfaces and often settle in depressions or grooves on the substrate (Crisp & Barnes 1954), and this can affect recruitment and survival. In particular, chthamalid recruitment and survival has been shown to be higher on rougher surfaces (Coombes et al. 2015). Research by Gallagher et al. (in prep) found that, in contrast to natural rocky shores in south-west Ireland, *Austrominius modestus* by far outnumbered native barnacle species on the majority of intertidal artificial structures surveyed. Densities of 228.2 *A. modestus* per 100 cm^2 were recorded on artificial structures in south-west Ireland, while native species only attained maximum densities of 161.1 per 100 cm^2 (*Chthamalus montagui*) and 32.5 per 100 cm^2 (*Semibalanus balanoides*) (see Figure 5). At the southern introduced limit of *Austrominius modestus*, while this species was found to be most abundant on an artificial structure (Farol, Ihla de Culatra, Algarve) at a mean density of 92.9 per 100 cm^2, it was by far outnumbered by the native *Chthamalus montagui* at the same site (752.0 per 100 cm^2) (Gallagher et al., unpublished data). Similarly, on the Isle of Cumbrae, Scotland, close to the northern introduced limit of *Austrominius modestus*, the native species *Semibalanus balanoides* by far outnumbered *Austrominius modestus* on artificial structures surveyed (Gallagher 2016).

Not only the size but also the type and age of the available substrate may be important. The majority of newer piers and slipways surveyed by Gallagher et al. (2015) were constructed from smooth concrete with few cracks or crevices, though over time, erosion of the substrate may produce a more heterogeneous surface. Older structures were composed of a rough conglomerate mixture or large stones, both of which have many cracks and crevices, which may be a factor promoting the recruitment and survival of native species. This may be due to the sheltered conditions created by the artificial structures themselves, which would promote the abundance of *A. modestus*, or it may be due to the ability of *A. modestus* to settle on smooth substrata, while natives prefer rough surfaces. At a site seaward of the Biological Station at Roscoff, France, Gollέty et al. (unpublished poster, 2008) reported higher densities of *A. modestus* on a concrete block (mean ± SE: 67 305 ± 16 371 m^{-2}, max. 84 960 m^{-2}) than on a granite boulder (mean ± SE: 16 923 ± 4680 m^{-2} versus 18 135 ± 4643 m^{-2} for *Chthamalus montagui*), which she suggested could be due to the predominantly smooth surface of the former. The concrete block was dominated by *Austrominius modestus*, with only about 1% cover of other barnacle species (*Chthamalus montagui* and *Semibalanus balanoides*) (Golléty et al. 2008). In the summer of 1997 and 1998, on a wall which was a mixture of natural stone and concrete at Roscoff, near Golléty et al.'s (2008) site, O'Riordan et al. (2001) had found cyprids and adults of *Austrominius modestus*, *Chthamalus montagui* and *C. stellatus*, as well as adult *Semibalanus balanoides*. Golléty et al. (2008) reported that in 2005, the recruitment period of *Austrominius modestus* occurred from late spring to the middle of autumn, with two peaks in June, another important one in August and a small one in October.

Levels of recruitment of *A. modestus* have been seen to vary also with intertidal shore height and subtidal depth. At Lough Hyne Marine Nature Reserve, SW Ireland, recruitment and survival were examined on machined-slate panels at 0 m (~two-hour emersion per tidal cycle), 6 m depth and 12 m depth at two sites with different flow regimes, over a three-year period (Watson et al. 2005). *A. modestus* was the species of barnacle that dominated the intertidal panels and had higher levels there than subtidally, with a maximum mean of ~two recruits cm^{-2}, but with significant differences between seasons. Although *A. modestus* recruited to the subtidal monthly and seasonal panels, none were present on the subtidal annual panels; instead, *Balanus crenatus* and *Verruca stroemia* dominated the latter, highlighting the importance of post-recruitment processes to the survival of *Austrominius modestus* subtidally (Watson et al. 2005). In the English Channel, recruitment of four species of barnacle, including *A. modestus*, was recorded in cleared vertical patches, with highest counts occurring along the coast of Sussex, with greatest recruitment at Selsey Bill (a mean of 16 and a maximum of 23 cm^{-2}). Generally recruitment was greater at the lowest of the three shore levels (MHWN, MTL and MLWN) (Herbert et al. 2007). Further north, in subtidal samples in Helgoland, Germany, recruitment was recorded from June–July to September–October (Anger 1978). Meadows (1969) reported 51% mortality of recently recruited (maximum of two months old) *A. modestus* on subtidal panels (60–120 cm below MLWS) at Rosyth, Scotland, which was lower that recorded for *Semibalanus balanoides* (90% and 83% from two other sites, Greenock and Mallaig).

Health status, natural enemies and anthropogenic threats

The health status of *Austrominius modestus* has been described briefly in a range of studies, but no definitive overview of potential parasites or pathogens has been compiled to date. While parasites and disease in the marine environment are increasing, a definitive overview of the health status of this barnacle species has not been carried out. However, this in part may be due to a lack of focus on this aspect of its biology which would require a range of diagnostic tests to do a full screen with large sample sizes and over a range of geographic locations. Of the studies that have been carried out, there has been a focus on the role of barnacles as reservoirs or potential predators of parasites.

Bacteria, including coliforms

Clements et al. (2013) screened a range of barnacle species including *Austrominius modestus* for a range of coliform species to determine if barnacles attached to mussels could act as reservoirs for human coliforms. They found that *A. modestus*, which had outcompeted native species in some of the areas being studied, contained much higher levels of coliforms relative to the native species and could act as reservoirs for these bacteria – potentially being transferred to mussels which would ultimately be consumed.

Other studies have focused on the control of bacteria in the culture of various barnacle life stages. Bacteria may develop during the rearing of larvae, so researchers often try to counteract this by adding antibiotics, for example, 0.01% chloromycetin (Barnes & Barnes 1974) or 0.4 mL of Crystamycin solution (Barker 1976, Tighe-Ford 1977) or penicillin-streptomycin solution (e.g. Stone 1988, 1989).

Commensals or potential parasites

Of those commensals or potential parasites that have been described most, one in particular, a microparasite, is the isopod *Hemioniscus balani*. Generally, this isopod, a parasitic castrator of a number of native barnacle species, disrupts egg production. Reports of the presence of this isopod are variable, as is the impact. Crisp & Patel (1960) examined the influence of the parasite *H. balani* on the moulting rhythm of *Austrominius modestus* collected from the Brixham, South Devon, location where Southward & Crisp (1954) had found a high level of infection. Although Crisp & Davies (1955) had shown that this parasite can cause castration in *A. modestus*, the presence of the parasite had no significant effect on the moulting rhythm of *A. modestus* or on that of the other three species tested. They examined ten *Austrominius modestus*, of which 50% were infected. In the large *Perforatus perforatus*, the parasite was shed with the cast (and may explain the low levels of *Hemioniscus balani* recorded in this species), but this did not occur in *Austrominius modestus* or the other two species.

During 1940–1950, when temperatures around Britain increased, there was an increase in the incidence of *H. balani* in the cold-water *Semibalanus balanoides*, as if the latter species had become more susceptible to infection (Little & Kitching 1996). Crisp & Molesworth (1951) reported that the incidence of infection by *Hemioniscus balani* was >50% in *Austrominius modestus* and *Amphibalanus amphitrite* in some areas of South Devon and South Wales, Great Britain. In their survey of the French coast in (August) 1967, at La Jetée d'Eyrac, at Arcachon, Barnes & Barnes (1968a) noted that ~2% of *Austrominius modestus* had a parasite resembling *Hemioniscus*. O'Riordan & Ramsay (1999) did not find any present *Hemioniscus balani* in the *Austrominius modestus* samples that they examined from Setúbal or Praia de Faro in 1998, nor was it found by the same authors at Alvor in 2013 (O'Riordan & Ramsay 2013), but barnacles were sampled in March/April only.

Another parasite that is found in *A. modestus* is the eugregarine *Nipyxioides elminii*, which occurs in the intestine (Ormières 1983). Goedknegt et al. (2015), in a study of disease risk under climate change scenarios, particularly temperature change, found that *Austrominius modestus* significantly reduced cercarial stages of the trematode *Renicola roscovita* in mussel beds (*Mytilus edulis*) through filtration, and this relationship was temperature dependent, with increased predation with increasing temperature. Cysts of the trematode *Maritrema gratiosum* (formerly *Maritrema arenaria*) have been recorded in *Austrominius modestus* at a number of locations in Ireland and Scotland (Gallagher 2016, Gallagher et al. in prep., Swain, 2019).

Overgrowth by other species

A number of species have been recorded overgrowing *Austrominius modestus*. On the upper reef at West Tamaki Head, Auckland Harbour, New Zealand, although some *A. modestus* could survive several months, being nearly completely covered by the mussel *Xenostrobus pulex*, eventually they were smothered by the carpet of mussels, underlain by silt (Luckens 1964, 1975). Similarly, the Auckland rock oyster *Saccostrea* (*Crassostrea*) *glomerata* often smothered *Austrominius modestus*, as well as other barnacle species (e.g. *Chamaesipho columna* and *Epopella plicata*) by growing over them. However, if, when the oyster spat had settled, there was little rock surface free (due to heavy barnacle cover), the attachment of the oysters became less secure over time, and they could be easily removed by the activity of other organisms. Some of the best evidence for interspecific competition for space was between *Austrominius modestus* and the alga *Corallina officinalis* on both vertical and horizontal cleared rock surfaces (Luckens 1964, 1975). Although *Austrominius modestus* settled first, it was smothered by *Corallina*. On transparent plexiglass panels, suspended at a depth of 1 m below a raft in Helgoland Harbour, Germany, overgrowing, mostly by the colonial ascidian *Botryllus schlosseri*, caused high mortality of *Austrominius modestus* in October 1977 (Anger 1978).

Predation

In its invasive range, a number of species have been shown to selectively predate native species before *Austrominius modestus*. It was reported that the nudibranch *Onchidoris* selected *Semibalanus balanoides* and neither it nor the dogwhelk *Nucella* predated on *Austrominius modestus* (Potts 1970), but Barnett (1979) showed that *Nucella lapillus* would predate on *Austrominius modestus*. However, in laboratory experiments, *Nucella lapillus* took greater numbers of *Semibalanus balanoides* than *Austrominius modestus*, unless the whelks had been starved (for ten months) (Barnett 1979). *Nucella* drilled the opercular valves significantly more often when predating on *Semibalanus balanoides* but prised open *Austrominius modestus*, suggesting that *Semibalanus balanoides* may be able to close its valves more securely or with greater force, hence the need for drilling. It was proposed that selective predation by *Nucella lapillus* on *Semibalanus balanoides*, rather than *Austrominius modestus*, may explain some of the initial success of *A. modestus* in NW Europe, as it could utilise bare space for settlement and then establishment, created by the mortality of *Semibalanus balanoides* (Crisp 1958). The preference for *S. balanoides* may be due to ingestive conditioning to the native barnacle species, or it may be because *S. balanoides* has a larger average size (Barnett 1979), which is in line with Connell's (1961a,b, 1970) classic research, where *Nucella lapillus* selected *S. balanoides* rather than the smaller *Chthamalus*.

Pollution and heavy metals

It has been suggested that *Austrominius modestus* can tolerate pollution more than most native species in Great Britain (Crisp 1958), thriving in dirty harbours, where other species are uncommon (Little & Kitching 1996). Rainbow (1987) has described the levels of heavy metals in barnacles, including information about which ones are stored versus excreted or used and their value as biomonitors of trace metals in coastal waters, since higher body concentrations are accumulated where there is greater availability in the environment. Zinc is accumulated by barnacles as zinc phosphate granules, which, according to Rainbow (1987), may be a form of detoxification, thereby storing the zinc in a metabolically unavailable form. Please see Thomas & Ritz (1986) for the composition of elements in the 'zinc' granules in *A. modestus*. Rainbow & White (1989) gave concentrations (ppm dry weight) for four heavy metals in the body of *A. modestus* collected from a single site, Southend, Essex, England: 4900–11 700 Zinc, 20–169 Copper, 244–1382 Iron and 41–50 Cadmium. Rainbow (1985) and Pullen & Rainbow (1991) have examined heavy metal levels in *A. modestus* from the same site, while Al-Thaqafi & White (1991) investigated the effect of shore position and environmental metal levels on body metal burdens from two sites in Wales – Menai Straits and Anglesey. Please see levels listed in Table 1 (pp. 410–411) of Rainbow (1987) for comparison with other barnacle species and Table 4 of Zauke et al. (1992) for metal concentrations in ten species of barnacles from different regions of the world.

The assimilation efficiencies of four heavy metals were compared when adult *A. modestus* (collected from Southend) were fed different phytoplankton and zooplankton (a copepod collected from Hong Kong waters) diets (Rainbow & Wang 2001). Assimilation efficiencies differed for three of the metals, and there were variations between the different diets. Modelling of the accumulation of Cadmium and Zinc by *A. modestus* predicted that >97% of each of the accumulated metal had been derived from dietary ingestion, with <3% from the dissolved phase. The interaction between Cadmium and Zinc accumulation in *A. modestus* has been examined also (Elliott et al. 1985). Rainbow & Wang (2001) noted that the assimilation efficiencies of certain trace elements from its diet tended towards lower values for *A. modestus* than *Amphibalanus amphitrite* and *Balanus trigonus* (see their Table 3, p. 245). They suggested that this may indicate differences in the digestive physiology of the two families, that is, Austrobalanidae versus Balanidae. Zauke et al. (1992) examined Cadmium, Lead, Copper and Zinc levels in adult *Austrominius modestus* collected from 17 sites in two harbours in the Auckland area of New Zealand and from a site at Omaha Beach, ~60 km north. In general, the metal concentrations in *A. modestus* were towards the lower end in comparison to European studies. They suggested that the high concentrations of Cadmium in the samples from the study's mangrove site (Omaha Beach) may be due to the naturally increased bioavailabilities of certain metals in mangrove systems.

In recent years, a number of authors have used *A. modestus* as a model or test species in pollution studies. In New Zealand, *A. modestus* was investigated as a possible indicator of water quality (Okemwa 1999), while in southern England, the effects and toxicity of chromated copper arsenate (CCA) wood preservative was tested for a range of invertebrate fouling organisms, including *A. modestus* (Brown & Eaton 2001, Brown et al. 2001). Greater settlement occurred on non-treated panels, but *A. modestus* was one of the species which was dominant on the treated panels. Hill & Holland (1985) examined the influence of oil shale on intertidal organisms. They found that *A. modestus* and *Semibalanus balanoides* were induced to settle. They suggested that fractionated extracts of the oil shell containing metalloporphyrins acted in a similar manner to arthropodin, binding the proteins associated with the cyprid attachment disc.

Geographic distribution and changes (historic and future predictions with climate change)

The spread of *Austrominius modestus* is one of the best-documented examples of the spread of a marine animal to a new range (Barnes & Barnes 1965b), and there have been many published records of its dispersal and abundance on European coasts, in particular from the time of its initial introduction to Europe until the late 1960s (e.g. see Lewis 1964). Its spread is a good example of the effect of ship fouling in extending the range of a species (Pyefinch 1950). As well as shipping (both adults fouling on hulls and larvae in ballast water), other vectors possibly responsible for remote dispersal of *A. modestus* are flying boats (M. Barnes pers. comm. in Eno et al. 1997) and shellfish, while marginal dispersal is through the pelagic larval stages. O'Riordan (2010) summarised its spread country by country, with relevant references and notes in the distribution table and the section on 'History of Introduction and Spread', so subsequently we have just summarised its spread, given the key references for its spread and highlighted any recent changes. The first published record of this species in Europe was in Great Britain, by Bishop (1947), who recorded very large numbers on the Admiralty Raft moored in the mouth of Chichester Harbour in July 1945. However, according to Crisp (1948), Bishop had seen it there in 1944, and Bishop (1951) stated that it was first discovered in British waters in 1944. Even so, when Stubbings (1950) re-examined collections made in 1944 of fouling organisms from ships, he suggested that *A. modestus* may have been present in the Portsmouth area since 1943, while Crisp (1958) thought that it could have been there since 1939. It is believed that *A. modestus* was transported to Britain via shipping, evidence for this coming from live specimens of *A. modestus* found on a ship in Liverpool which had returned from Australia and New Zealand (Bishop 1947). Crisp (1948) reported *A. modestus* in Essex in autumn 1945, suggesting that, based on their size, they had settled in spring of 1945. Crisp & Chipperfield (1948) also recorded *A. modestus* from the south coast in 1945. In summary, the distance between the initial locations of colonization, along with the subsequent extent of range expansion, led Stubbings (1950) to suggest that *A. modestus* was well established prior to 1945, but the Second World War may have prevented the early stages of the introduction of this species from being recorded in British waters (Crisp 1958).

It was suggested by Crisp (1958) that the initial settlements in British waters must have been of a large number of individuals, which subsequent research confirmed (Flowerdew 1984, Dando 1987). An electrophoretic examination of *A. modestus* from ten European versus three Australasian populations found that the allele frequencies in all samples were similar (Flowerdew 1984). The genome of European *A. modestus* was entirely representative of the Australasian population, indicating that over the 40 years since its establishment, natural selection and genetic drift did not produce any changes great enough to produce genetic variation. There must also have been little differential selection on the European populations compared to those in the southern hemisphere. No significant differences in allele frequencies were seen between samples from Scotland to northern Spain (Flowerdew 1984) or between Cork Harbour and Bantry Bay, southern Ireland (O'Regan 1980).

There are many records following the spread of this species in Great Britain (see Southward 2008, for a summary of its distribution in Great Britain) that describe the spread of the species. In 1948, *A. modestus* was established, but not common, in the Helford River, Cornwall, on oyster grounds (Knight-Jones 1948). *Austrominius modestus* was not present on Skomer Island in the Bristol Channel during a survey in 1946 (Bassindale 1947), being first reported in the Bristol Channel at Blue Anchor (see Bassindale 1947) and near Cardiff by 1947, but in low abundances, indicating that *A. modestus* was just becoming established at this location (Purchon 1947). By 1948, *A. modestus* was the dominant barnacle in the intertidal zone and more widespread than native species of barnacles in the south-east of Great Britain. Additionally, it was found in areas unoccupied by native barnacle species, for example, Maldon beach (Knight-Jones 1948) or co-habiting on artificial substrates with native species (e.g. on pier piles in the Mersey estuary [Corlett 1948]). In Chichester Harbour, *A. modestus* was noted to be the most abundant barnacle species in the harbour by the 1950s (Stubbings & Houghton 1964). In 1952, two specimens were recorded at Ramsey, on the Isle of Man, where, by 1955, it was common and present further south (see Bruce et al. 1963). By 1957, *A. modestus* was recorded to be present in the Plymouth area (Marine Biological Association 1957), while Crisp & Southward (1959) examined its spread up until 1959. In 1963, it was absent from the open coast of the Dale Roads area of Pembrokeshire but was recorded as spreading within Milford Haven and increased in abundance at Watwick Bay and Dale Point (Moyse & Nelson-Smith 1963). *Austrominius modestus* was common in the Blackwater and Colne estuaries in the south-west of England, being the dominant barnacle in the Blackwater estuary in the 1960s (Davis 1967). Since the 1970s, there have been few new reports on the distribution and abundance of this invasive species in Britain. *Austrominius modestus* was most common in sheltered areas of North Wales, in particular in the Menai Strait. Although *A. modestus* occurred all around Anglesey, it was most common in sheltered areas of North Wales, and only in the Menai Strait did it make a significant contribution to barnacle cover (Bennell 1981). In the inner Bristol Channel, *A. modestus* was recorded from large boulders of Porlock Bay in 1980 (Hiscock 1986). Larvae of *A. modestus* were reported to be rare in waters off the Isle of Man in the early 1980s (Salman 1982). The most northerly records in Great Britain are from a number of sites in the Shetland Islands, as reported by Hiscock et al. (1978), where it had disappeared by 1986, but it has been found there recently attached to drifting plastic (Barnes & Milner 2005). It has been recorded on Scottish islands, such as the Isle of Cumbrae (Connell 1955, O'Riordan et al. 2009) and the Outer Hebrides (Howson et al. 1994).

Southward (1991) examined how the intertidal abundance of *A. modestus* had changed over 40 years in south Devon (Cellar Beach, River Yealm) from its first record there in 1948. Although it increased in abundance in the 1950s, it then stabilised at a low level of abundance. There were large fluctuations in density, which were not directly related to temperature, but may instead be due to the number of larvae available for settlement. Southward (1991) suggested that these larvae could have originated from breeding populations in the sublittoral or in the Tamar and Plym estuaries, where lowered salinity encouraged greater densities than in the River Yealm. Arenas et al. (2006) recorded *A. modestus* to be present at 66% (8) of their 12 sites surveyed using a rapid assessment survey on the south coast of England during 2004.

Based on 1954–1956 surveys, in the eastern part of the English Channel, *Semibalanus balanoides* was replaced in sheltered harbours and bays by *Austrominius modestus,* but *A. modestus* was common only in the estuaries and harbours in the west (Crisp & Southward 1958). Initially, headlands, such as Peveril Point, Portland Bill and Cap la Hague (at the tip of the Cotentin Peninsula), being more wave exposed, presented hydrographic barriers to its westward spread, slowing its spread by marginal dispersal. Hemingway-Jones (1961), citing Crisp & Southward (1953), suggested that *A. modestus* cannot disperse further than 48 km by marginal (coastal dispersal) and that they might spread 20–30 km per annum along an open coast. When the abundance of four species of barnacles at three heights in the intertidal along the central south coast of England was surveyed between 1994 and 1999, including sites previously surveyed by Crisp & Southward (1958), Crisp et al. (1981) and Southward (unpublished), Herbert et al. (2007) found that *A. modestus* was most common in the eastern English Channel, especially near estuaries (see their Figure 5). The maximum abundance was 4 cm^{-2} (at MHWN, at Southsea). At some sites east of Portland Bill, abundance was similar to that recorded some 40 years earlier (Crisp 1958, Crisp & Southward 1958). However, further west at Lyme Regis, where between 1948 and 1958 the species was absent, it was now ‘occasional’, and at Brixham, it was ‘abundant’ when previously it was ‘occasional’.

Following its introduction to Great Britain, this species spread rapidly along European coasts (e.g. Crisp 1958, Harms & Anger 1983), but cold winters constrained its spread. *A. modestus* was noted to be common on the southern North Sea coast of The Netherlands by Boschma in 1948, having been first recorded from The Netherlands in 1946 (van der Meulen 1946, Bishop 1947, Boschma 1948, Leenhouts 1948a,b, Hartog 1953, 1955), but may have first settled at the Hook of Holland in 1945 (Hartog 1953). Please see Figure 2, p. 13, of Hartog (1953) for its spread along the Dutch coast up to 1951. It had spread to Belgium by 1950 (Hartog 1953, Leloup & Lefevere 1952). It was found in France in 1950 also (Hartog 1953, Bishop 1954), but may have been in Normandy since 1944 (Hartog 1956) and was recorded settling in large numbers in Roscoff, Brittany, in summer 1952 (Hartog 1953, Drach pers. comm. in Bishop 1954). It was recorded in Helgoland in 1954 (Hartog 1959, Kühl 1963), the Isle of Sylt in 1955 (Kühl 1963) and had reached its northern continental border in southern Denmark by 1978 (Theisen 1980, Harms & Anger 1989). The Danish Wadden Sea was recorded as the northern limit of *A. modestus* in Europe at that time (Theisen 1980), but it died out there during the cold winters (Jensen & Knudsen 2005). Cuxhaven by Kühl (1963) also reported sensitivity to cold winters. Similarly, in some shores in France (Barnes & Barnes 1966), a severe winter in 1962–1963 caused high mortality, as well as in *Perforatus perforatus* (80%–90%) and ‘*Chthamalus stellatus*’ (5%–90%) (Barnes & Barnes 1966). However, it was recorded there every year between 2004 and 2008, being found near the eastern entrance to Limfjord in 2007 (Jensen 2009), so less cold winters allow it to re-establish in areas. In Helgoland, in the German Bight area, it has become dominant, although native species continue to persist (Franke & Gutow 2004, Reichert & Buchholz 2006, Witte et al. 2010). In Danish waters, *Austrominius modestus* now extends through the Limfjord (Jutland) and into the N.W. Kattegat (J.G. Lützen & H. Glenner, in prep., pers. comm. to O’Riordan, 28th November 2019).

Similar to its gradual spread northwards, *A. modestus* gradually colonized southwards. Crisp & Southward (1958) suggested that in 1954–1956, the European range of *A. modestus* extended from the south-west of Scotland to France, but it had actually been recorded in Galicia, northwest Spain, in 1955 (Fischer-Piette & Prenant 1956). Based on a survey in 1954, *A. modestus* was well established on the French coast from the Rade de Brest to the estuary of the Jaudy and from Cap de la Hague to the Belgian border (Bishop & Crisp 1957). Single specimens were found at some other locations along the French coast, though not further south than St. Jean-de-Luz. The authors remarked that even though there was suitable habitat and high levels of shipping activity, this species had not spread further south at that time. Bishop et al. (1957), Bishop & Crisp (1958), Fischer-Piette & Prenant (1956) and Crisp & Fischer-Piette (1959) provide other records of the occurrence of *A. modestus* on the French coast. Additional surveys carried out in 1957 reported increases in the abundance of *A. modestus* around Concarneau and Lorient (Crisp 1959b). It was suggested that the French populations were not established via spread from Belgium and The Netherlands, but they were separately established via shipping from Britain (Bishop & Crisp 1957). Additionally, the establishment of *A. modestus* in The Netherlands was unlikely through dispersal from France, but a separate colonization event (Bishop & Crisp 1957). Surveys in the 1960s monitored its progress south (e.g. Fischer-Piette & Forest 1961, Fischer-Piette 1963, 1964, 1965, Barnes & Barnes 1965b, 1966). *Austrominius modestus* was first recorded in Arcachon, France, in 1964 (Barnes & Powell 1966), following which it became highly abundant, being the most common barnacle species at this location, having smothered natives in some locations, colonizing areas previously unoccupied by native barnacle species (Barnes & Barnes 1968a). *Austrominius modestus* was established further north in the Baie de St. Malo (Barnes & Barnes 1969), though the coast north of Granville was thought not to be ideal for the establishment of this species, and only a small population survived there. South of Arcachon, *A. modestus* was established at St. Jean-de-Luz (Barnes & Barnes 1969). In 1971, *A. modestus* was found further south on the French coast, including Socoa, near the border of north-west Spain (Barnes et al. 1972). When its abundance was surveyed on 17 shores, between Calais and the Gulf of Malo, Cotentin Peninsula (Herbert et al. 2007), including sites previously surveyed by Crisp and Southward (1958), Crisp et al. (1981) and Southward (unpublished), *A. modestus* had increased by between one or two orders of magnitude on the west side of the Cotentin Peninsula compared to in 1954 when Crisp & Southward (1958) reported the barnacle as 'rare' or 'occasional'. In the 2001 and 2002 surveys, it was not found at one of the French sites surveyed and was 'abundant' at just one site, Calais, the most easterly site of those that they surveyed. This species is present in the Bassin de Thau, on the French Mediterranean coast, extending its known eastern European limit (O'Riordan & Ramsay 1999, citing Zibrowius, pers. comm.). However, Buckeridge & Newman (2010), also citing Zibrowius (pers. comm.), pointed out that the Thau population is small and may depend on yearly imports of oysters from the Atlantic coast of France. Back in 1968, Barnes & Barnes (1968a) had indicated the importance of activities associated with oyster cultivation for its spread within the Arcachon Basin, France.

A single individual was recorded in South Africa in 1949 (on an experimental plate at a depth of ~60 cm in Cape Town Docks); however, the species did not become established in this area (Sandison 1950). Tøttrup et al. (2010) described *A. modestus* as being a 'naturalised' member of European intertidal habitats. Although it has not yet been reported from the coasts of America, the reason for which remains unclear, it is expected to become established there in the future, if it has not already done so (Carlton et al. 2011).

The spread of *A. modestus* along the Atlantic coasts of Spain and Portugal between 1955 and 1963 was well documented (Barnes & Barnes 1965b, Fischer-Piette & Prenant 1956, 1957, Fischer-Piette & Forest 1961). In 1963, the southern limit of this species in Europe was recorded as São Martinho de Porto, Portugal (Barnes & Barnes 1965b). Eno et al. (1997) suggested erroneously that it occurred as far south as Gibraltar, citing Barnes & Barnes (1966), but although Gibraltar is the station furthest south that Barnes & Barnes (1966) surveyed in Spain (as well as surveying Huelva, Cadiz and Barbate along this coast), they do not mention *A. modestus* occurring there. They refer back to their earlier paper (Barnes & Barnes 1965b) for the detailed distribution and abundance levels for *A. modestus*, where they categorically state that in 1963, it was not found on the southern coasts of Spain (or France). Intertidal surveys on seven shores from Tarifa to Almuñecar, in Andalusia, Spain, in January 2018 failed to find any *A. modestus* (O'Riordan & Ramsay, unpublished). O'Riordan & Ramsay (1999) confirmed its southern European continental limit in Portugal to be Faro. Currently, the European range of *A. modestus* is from Scotland (The Shetlands) and Denmark in the north to Ilha de Culatra, near Faro, Portugal (Gallagher unpublished), in the south and two locations in the Mediterranean Sea (Zibrowius pers. comm., Casellato et al. 2007). The most easterly location reported is by Casellato et al. (2007), who recorded it in their surveys of subtidal (22–24 m deep) ‘tegnúe’, rocky outcrops in the Gulf of Venice, in the Northern Adriatic Sea, Italy, carried out between 2002–2003; however, this record has not been reported in the ICES WGITMO national reports, and this depth is much deeper than the species has been found elsewhere. A single specimen was found at Funchal marina, Madeira, in May 2005 (Wirtz et al. 2006), so it was listed as not established there (Chainho et al. 2015). Boaventura (2000) and Boaventura et al. (2002) did not mention the occurrence of *A. modestus* on any of the 27 rocky shores that they surveyed in spring 1997. As part of the INSPECT project, Cruz & Castro (2011) surveyed 24 sites on the Portuguese coast for *A. modestus* in spring/summer of 2010 and 2011. Its occurrence was mostly associated with ports and estuaries, and they recorded three new locations for it on the western Portuguese coast (Cruz & Castro 2011, pers. comm. to R. O’Riordan). Gallagher (2016) surveyed 18 shores in the Algarve in 2014 and found *A. modestus* present on all but two of the shores. However, when O’Riordan & Ramsay (unpublished) resurveyed 12 of the same shores in May 2018 and April 2019, *A. modestus* was absent from six of these shores.

At the limits of the geographical range of a species, the abundance and exact range can fluctuate (Southward & Crisp 1956). These fluctuations can often be linked to environmental changes, and by investigating this, the relative importance of these factors in determining the species distribution can be determined. Unpublished research carried out by Gallagher et al. examined the factors controlling the success of *A. modestus* at its southern limit in the Algarve and close to its northern limit on the Isle of Cumbrae, Scotland (see previously re: Shetland Islands as well). At the northern location, strong competition exhibited by the native species *Semibalanus balanoides* during years of good settlement for this species was limiting the abundance of *A. modestus*, while at the southern limit, it seems likely that desiccation stress, or some other stress, at the settlement and recruitment stage is limiting the abundance of *A. modestus*. Previously, it had been suggested that high temperatures were responsible for restricting it to the lower shore of some Atlantic shores in SW France and in some rias in Spain (Barnes & Barnes 1966, Barnes et al. 1972).

Ireland is the most westerly location of *A. modestus*, where it was first recorded in 1957 (Beard 1957). O’Riordan (1996, 2002, 2010) described its spread around the coast in the subsequent 50 years. The intertidal distribution and abundance of *A. modestus* around the Irish coast changed between the 1950s and 2003 (Simkanin 2004, Simkanin et al. 2005). It was found on 57 of the 63 sites resurveyed, and its abundance showed an overall increase, especially along the east coast. The significant increase of *A. modestus* over this period of time was suggested to be a classic example of a successful invasion, reflecting a rapid colonization of a new area unrelated to climate change (Simkanin 2004). However, studies have shown that climate change may indirectly affect the interactions between introduced and native species by causing increased stress in native populations (Occhipinti-Ambrogi & Savini 2003) and earlier recruitment in introduced species (Stachowicz et al. 1999), thus facilitating the expansion of non-native organisms. Although Simkanin (2004) cautioned that this apparent increase may be an artefact due to operator error, rather than a change due to natural or anthropogenic reasons, other studies supported that *A. modestus* has increased its range significantly around the Irish coast (O’Riordan 1996). Subsequent reports describing increases in the abundance of *A. modestus* with warming sea surface temperatures (e.g. Lawson et al. 2004, Allen et al. 2006, Witte et al. 2010) have suggested that *A. modestus* could be an ‘ecological sleeper’ (Witte et al. 2010), with the potential for further increases in abundance towards the northern part of its invasive range with predicted climate change. While this may be the case in the middle and northern parts of the invaded range of *A. modestus*, data collected in the Algarve (Gallagher 2016) make it unlikely that warming temperatures will facilitate an increase in the abundance of this species at very southerly locations. Although *A. modestus* appears as tolerant as *Chthamalus montagui*, its restriction to lower on the shore than *C. montagui* towards the south of its range may be because the temperature conditions are becoming too extreme (Barnes et al., 1972). Some surveys of the intertidal Moroccan coasts during spring tides have been carried out recently by researchers from the University of the Algarve (pers. comm. to R. O'Riordan, May 2018). It will be interesting to see whether *Austrominius modestus* is present in any of their catalogue of photographs from these shores, which would experience higher temperatures than in the Algarve.

Ecosystem structure

Although invasive species generally have negative associations, it is not always the case in reality, and there have been very few recorded extinctions due to competition from invasive species, and where extinctions do occur, it is generally between trophic levels, for example, predator and prey (Davies 2003). A review by Katsanevakis et al. (2014) noted that many invasive species have both positive and negative impacts and that the positive impacts are largely underestimated. Species richness is not necessarily an indicator of ecosystem function (Schwartz et al. 2000); therefore, if *Austrominius modestus* reduces the number of native barnacle species, this may not alter ecosystem function, provided that *A. modestus* plays the same functional role as those native species. The overall impact of *A. modestus* on the dynamics of rocky shore communities in Great Britain has been small (Raffaelli & Hawkins 1996). It simply replaced some individuals of a group or a guild of co-occurring barnacles (e.g. *Chthamalus montagui*, *C. stellatus* and *Semibalanus balanoides*), which were seen to fluctuate in abundance over a 40-year period from 1951–1991, changing sea temperature being one of the potential factors involved (Southward 1991).

Austrominius modestus has been found to coexist with native barnacle species at multiple locations (e.g. see Gallagher et al. 2015, 2016, 2017). This could be facilitated in various ways, for example, *A. modestus* and native barnacle species display distinct patterns of zonation and generally occupy different parts of the shore. Colonization of different parts of the shore reduces direct competition between the species, allowing them to coexist. Differences in the timing and extent of the reproductive periods of the native and invasive species are also likely to be a contributing factor in the coexistence of these species, with *A. modestus* and native barnacle species essentially utilising different temporal niches. It was noted that where *A. modestus* started to become dominant, it was probably because of greater fecundity and prolonged breeding and settling seasons, enabling prior colonization of vacant sites on the substrate (Foster 1970). Shinen & Navarrete (2014) reported that the barnacles *Notochthamalus scabrosus* and *Jehlius cirratus* coexist neutrally. They found that a lottery for space during settlement largely determined the distributions of the two species. Small, nonsignificant and probably ephemeral fitness differences, which were inconsistent across the tidal gradient, probably provided enough niche differentiation to allow coexistence (Shinen & Navarrete 2014).

Within three years of settling in parts of the Firth of Forth, Scotland, *Austrominius modestus* had started to outnumber the former dominant species *Semibalanus balanoides* (Hemingway-Jones 1961). Sometimes later settlements of *Austrominius modestus* attached amongst spat of *Semibalanus balanoides*, and because the latter were faster growing and took up lateral space, the *A. modestus* have to project themselves above the *S. balanoides* (Crisp 1960a). If these *Austrominius modestus* survived, they could grow rapidly, mature early and could cause the underlying *Semibalanus balanoides* to become silted up and smothered (Crisp & Davies 1955, Crisp 1960a). Towards the northern part of its introduced range, such as western Scotland, where winter temperatures are low and summer temperatures are only moderate, native *S. balanoides* may be at an advantage in competition with *Austrominius modestus*, since at these temperatures, brood production by the latter species is relatively low (Barnes & Barnes 1962). However, further south, the ability of *A. modestus* to reproduce and settle throughout the year, unlike *Semibalanus balanoides*, gives it a greater chance to settle high on the shore and grow during more favourable climatic conditions (Foster 1971a,b). Settlement over the autumn and winter, when desiccation stress is less, may establish the ascendancy in intertidal distribution, with the upper limit being maintained by those individuals which grow sufficiently to reach a size which will protect them from lethal dehydration when adverse emersion conditions arise at that level (Foster 1971a,b).

Working with mathematical colleagues, the authors (Gallagher et al., 2020), have modelled the colonization of space by *Semibalanus balanoides* and *Austrominius modestus* in 1) communities where the species are initially present at different densities, 2) on a novel substrate and 3) under the scenario of future climate change. The time difference between the peak of *Semibalanus balanoides* reproduction and *Austrominius modestus* reproduction is the key factor in determining whether the two species coexist or outcompete one another. The longer the time period, the more *Semibalanus balanoides* is favoured. This is most likely because this allows *S. balanoides* more time to utilise space, especially as the recruits grow more quickly; thus, there is a lower likelihood of them being displaced by *Austrominius modestus.* A key factor with respect to the occurrence of a novel substrate is when it becomes available relative to their respective reproduction and recruitment. Finally, based on the models, the gradual warming of waters, which would positively affect *A. modestus*'s reproduction, generally favours *A. modestus*, leading to a reduced density of *Semibalanus balanoides* and eventually its extinction. Interestingly, for some parameter values, a more complex scenario is plausible due to warming, which may favour *S. balanoides* first, but then the trend reverses again, leading to the complete elimination of *S. balanoides.*

Since native barnacle species have a lower tolerance of disturbance, *Austrominius modestus* can achieve high abundance in harbours and ports on both artificial and natural substrates and occur at shore levels where native species would outcompete it on rocky shores. At the lower shore, on European shores, there is some competition for space between *A. modestus* and the native *Balanus crenatus* and *Amphibalanus improvisus* (Crisp 1958, Kühl 1963, Foster 1970), as well as higher up with *Semibalanus balanoides* (Kühl 1963). However, in the case where there are no native barnacle species present, *Austrominius modestus* is capable of colonizing the entire range of the intertidal zone (as well as subtidally), though not at exposed locations. Similarly, because *A. modestus* can tolerate low salinities and turbid waters, Barnes & Barnes (1968b) suggested that in some very protected areas in harbours or quiet bays (in SW France and southern Spain), where the water was very turbid and the salinity was relatively low, '*Chthamalus stellatus*' could be restricted to higher shore levels due to competition with *Austrominius modestus* (see also Barnes & Barnes 1966), as well as *Amphibalanus improvisus and Amphibalanus amphitrite. Austrominius modestus* competes with all of the other species of barnacle in Belgian waters (Kerckhof 2002).

Determining the functional role of *A. modestus*, and comparing this with native barnacle species, is of key importance in determining the ecosystem level impact of *A. modestus. Austrominius modestus* plays a similar functional role to natives (Olenin et al. 2007). However, while it has not been investigated in detail, there is some evidence that the *A. modestus* may differ from the native species in its utilisation of food resources (Southward 1955a,b, Moyse 1963, Stone 1989, Harms 1999). This may be due to differences in rate of cirral beat (Southward 1955a,b), potential differences in diet (Stone 1989) and contribution of larvae to the plankton community. If so, these could mean that *A. modestus* plays a different role to native barnacle species, which could facilitate niche partitioning, but this is currently speculative. There are some known key differences in the niche occupied by *A. modestus* and native barnacle species, which also play an important role in facilitating coexistence (see Figure 6).

Austrominius modestus is most often found in sheltered, estuarine areas, with highest abundances at the middle and low shore levels. This species can persist in areas that are subject to high levels of disturbance, due to its opportunistic nature, which is typical of invasive species (see Figure 7). Although the native species *Semibalanus balanoides* is also found at the middle to low shore, *S. balanoides* is more tolerant of wave-exposed conditions and less tolerant of estuarine conditions (especially low salinities) in comparison to *Austrominius modestus. Chthamalus montagui* dominates at the high shore level, generally at more wave exposed locations (but being replaced by the native *Chthamalus stellatus* on the most exposed shores) and does not have a

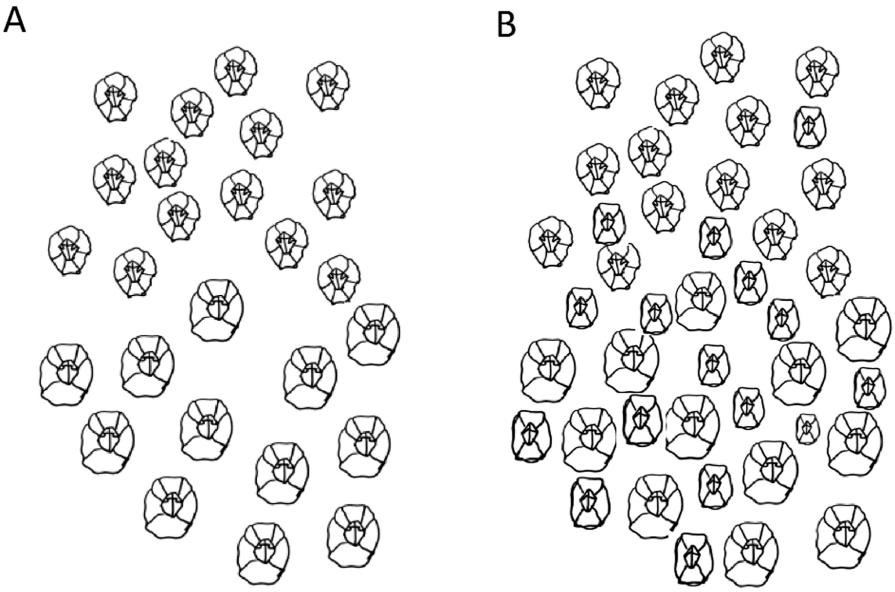

Figure 6 Generalised illustration of typical distribution of barnacles on the shore (high to low = top to bottom) (A) prior to *A. modestus* invasions and (B) after. See Figure 7 for the identity of the three species.

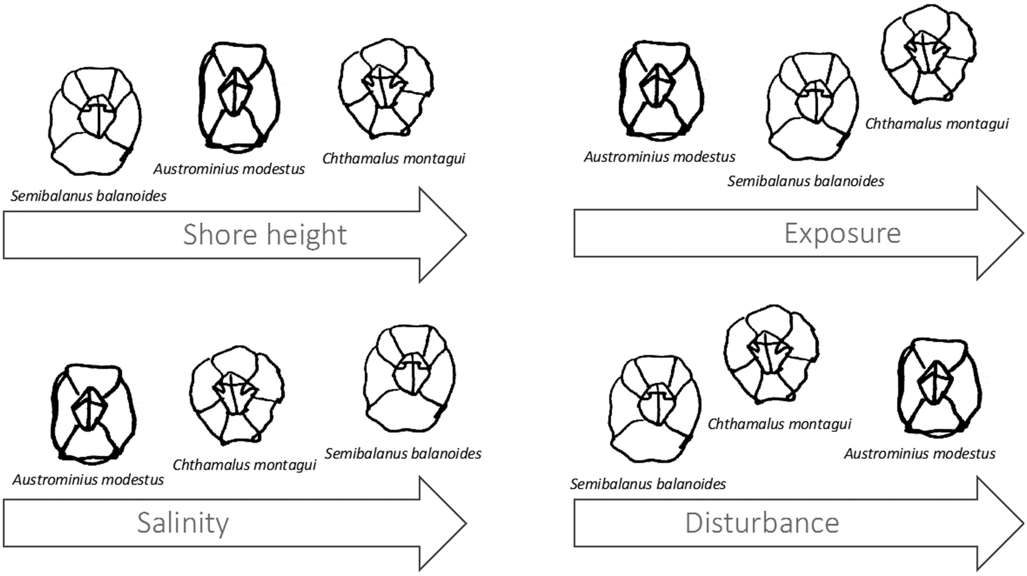

Figure 7 Indication of the varying tolerance levels of *Austrominius modestus, Semibalanus balanoides* and *Chthamalus montagui* to four different environmental variables as they increase from low (left of figure) to high (right of figure)

high tolerance of estuarine conditions. When the distribution of barnacles at three shores height on two sheltered and two exposed intertidal shores was examined in the Plymouth region, it was chthamalids that dominated, with *Austrominius modestus* reaching a maximum of 25% (Jenkins 2005). However, high densities of *A. modestus* have been recorded at some locations; for example, between 1959 and 1965, *A. modestus* was one of the most important organisms on the sea walls in the intertidal of the Blackwater estuary and adjacent waters in Essex, as well as on stones and shells amongst the muddy sand, being very common in the Colne estuary, mostly on the lower and middle shore but also subtidally. In the Blackwater estuary, it was the dominant barnacle species, reaching densities of up to 3750 individuals per m^2 (Davis 1967). Forty years later, at one of their sites in Roscoff, France, Gollety et al. (2008) recorded densities of 84 960 *A. modestus* m^{-2}, which they said was comparable to the densities seen for the other commonly occurring intertidal barnacles, *Chthamalus montagui*, *C. stellatus* and *Semibalanus balanoides*, on Atlantic European shores. They mentioned that common to abundant densities can be observed along the coasts of Brittany, France, with densities from 13 040 to 77 200 m^{-2} around Roscoff, while Barnes (1971) recorded 40 000 *Austrominius modestus* m^{-2} in the Arcachon Basin.

As mentioned previously (see section on Substrate type for *A. modestus* under 'Settlement and recruitment'), *A. modestus* is known to attach to a wide range of substrata, including other living organisms. In its native range in New Zealand, it was reported that it could smother and kill mangrove seedlings (Moore 1944). It is currently not known if there is a similar effect of smothering on native species in its invaded range through either competition for space or even smothering. In the early years after it was reported in Great Britain, concern was expressed because it was found to settle prolifically on panels during and after oyster spatfall so that it was competing more keenly with the young spat than any native barnacle species or sessile forms, and poor growth of young oyster spat was attributed to competition with *A. modestus* (Knight-Jones 1948). Although oyster spat could grow over and smother nearby *A. modestus*, the resultant oysters became misshapen and stunted. At that time, there was concern that it might cause problems for oyster cultivators in France and The Netherlands, where they were using artificial spat collectors exposed at low tide (Knight-Jones 1948), but there is nothing subsequently in the literature about this potential conflict. Settlement of *A. modestus,* as well as other barnacle species, on oysters and edible winkles was also reported to be a problem for the shellfish industry in Great Britain. Fouling by *A. modestus* caused complaints by sellers of winkles there (Anon 1948), for example, in West Mersea (Knight-Jones 1948), since the trade was accustomed to receiving clean winkles and most of the fouling was due to *Austrominius modestus*. There were complaints from oyster dredgers who had to remove *A. modestus* before selling (Knight-Jones 1948). Finally, concern was expressed that *A. modestus* might retard the recovery of oyster beds on the east coast of England, which had been affected by non-native *Crepidula fornicata* and *Urosalpinx cinerea*, followed by a severe winter (Knight-Jones 1948).

The question remains whether the presence of *Austrominius modestus* has a negative impact on ecosystem function. If not, and this species carries out the same functional role as native barnacles, its presence could potentially be seen as positive, as it could act as a replacement for *Semibalanus balanoides* under future climatic situations if *S. balanoides* dies out. The presence of generalist non-native species may contribute to ecosystems that are better able to cope with future environmental change (Witte et al. 2010). In the absence of this non-native species, only chthamalid barnacles would be present. There are some indications that there are differences between *Austrominius modestus* and native barnacle species that could have the potential to alter ecosystem function, but this needs to be confirmed. Baird et al. (2012) assessed the impact of *A. modestus* (and another invasive species there, the Pacific oyster *Crassostrea gigas*) on the structure and function of the entire intertidal region of the Sylt-Rømø Bight ecosystem (~87% of the Bight was declared a World Heritage Site by UNESCO in July 2009). Quantified network models with carbon (a surrogate for energy) were constructed to represent three different time periods. Changes in system attributes between 1995 and 2007 were ascribed to the impact of the invasive species on organisation and function of the system. For example, when there was a high biomass (1.3 and 15 gC m^{-2} of *Austrominius modestus* and *Crassostrea gigas*, respectively) of these two invasive species in 2007 (having increased from virtually zero in 1995), they accounted for ~35% of the total phytoplankton uptake, which then impacted lower trophic levels. However, the biomass of both species declined by 2010, following an unseasonably cold 2009/2010 winter, to only 0.12 and 0.6 gC m^{-2}, respectively.

Overall, the presence of generalist non-native species and the absence of specialist native species may lead to negative impacts on local biodiversity. In this specific case, it is important to consider the potential positives of the presence of *Austrominius modestus* but also to be aware that this species could have increased negative impacts at certain locations in the future. Hence, we encourage researchers to carry out more work on the biology and ecology of this species in its native range but especially at the current limits of its introduced range.

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