HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 52, 347–357 (1999)

The recent arrival of the oceanic isopod *Idotea metallica* Bosc off Helgoland (German Bight, North Sea): an indication of a warming trend in the North Sea?

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ABSTRACT: In 1988 a long-term study was started of the isopod fauna associated with surface drift material off Helgoland (German Bight, North Sea). In the summer of 1994 specimens of *Idotea metallica* Bosc were recorded for the first time. There is no evidence that this species has ever been present in the German Bight before. The samples contained males, both gravid and non-gravid females, and juveniles, indicating that the species reproduced successfully in the Helgoland region. Interbreeding of specimens from Helgoland and the western Mediterranean produced fertile offspring. As a neustonic species, *I. metallica* shows a high natural capacity for dispersal. It thus seems unlikely that the arrival of the species in the North Sea resulted from an accidental introduction by man. We are probably witnessing an extension of the species' geographical range by natural means of dispersal, as a response to recent changes in the ecological conditions of the German Bight. Temperature data measured by the Biologische Anstalt Helgoland since 1962 show that the last decade (except 1996) was characterized by unusually mild winters. Following the severe winter of 1996, *I. metallica* was again absent from the Helgoland region. After the subsequent mild winters (1997 and 1998), however, the species reappeared in the summer of 1998 with higher numbers than ever before. This suggests that the observed phenomena are closely connected with the recent temperature anomalies. *I. metallica* can be regarded as a potential immigrant to a warmer North Sea, and may be useful as a sensitive indicator of the predicted long-term warming trend.

INTRODUCTION

Changes in the geographic ranges of species and thus the appearance of species in, and their disappearance from, particular areas, is a phenomenon as old as life itself, driven by gradual evolutionary changes of the species, interacting with environmental changes such as those in climate. It is only with the rapidly increasing impact of humans on the earth's ecology, however, that the pace of change in the distribution patterns of species has increased dramatically (Hengeveld, 1990).

In general, the arrival of a species at a locality where it has not been found before can result from the following processes:

1. The species has undergone some evolutionary change in its genetic make-up, enabling it to extend its range to localities where it has not been able to exist before.

2. The ecological conditions in a particular locality have changed, whether for natural reasons or as a result of human activities, in such a way that a species will experience favourable living conditions in places where this has not been the case before.
3. The species (often assisted accidentally or intentionally by man) has succeeded in overcoming barriers to dispersal which have prevented it in the past from gaining access to and colonizing other suitable localities.

Surface drift material (mainly uprooted macroalgae) represents a specific neustonic habitat which provides a considerable number of macrofaunal species with a substrate to cling to, shelter from pelagic predators, and/or food. Although accumulations of drift material are common in many coastal regions, they have not yet attracted much attention in ecological research (Tully & Céidigh, 1986; Locke & Corey, 1989). Isopods are a significant macrofaunal element inhabiting drift seaweed. During a long-term study of the isopod fauna associated with drift seaweed, we recorded individuals of a species, *Idotea metallica* Bosc, which has never been recorded before in this area.

The geographical distribution of *I. metallica* was described by Naylor (1957). Resident breeding localities are the east coast of North America (from Florida to Nova Scotia) as well as the Mediterranean and Black Seas (Dow & Menzies, 1958; Abelló & Frankland, 1997). Furthermore, there are occasional records from many other parts of the world, from tropic, subtropic, temperate and even cold waters. However, it is impossible to decide from the literature data whether these records indicate the existence of further resident breeding populations. *I. metallica* is principally a surface dweller, associated with drift material such as weed and timber. It is this habit which confers a high potential for dispersal on the species and probably accounts for the species' nearly cosmopolitan distribution.

In the present paper we report on our records of *I. metallica* off Helgoland from the summer of 1994 up to now (summer 1998). Crossing experiments were performed to study whether North Sea and Mediterranean specimens of *I. metallica* really belong to the same species. Finally, data on water temperatures at Helgoland were analysed to look for possible causes of the observed phenomena.

MATERIALS AND METHODS

The hydrographic situation and the topography of the Helgoland region give rise to the formation of characteristic boundary zones between tidal currents of different speed and/or direction. These zones develop both south and north of the island. Along these zones, surface drift material accumulates. This is particularly evident during periods of calm weather, i.e. particularly in the summer. The accumulation of drift material occurs mainly south of the island when the tide rises, and north during the falling of the tide. The accumulating material is composed mainly of uprooted macroalgae such as *Fucus* sp., *Ascophyllum nodosum*, and, to a lesser extent, *Sargassum muticum* and *Himanthalia elongata*. Much of the macroalgal debris found off Helgoland probably does not originate from the rocky island itself but is carried along by water currents from coastal regions of Britain and the Wadden Sea area. Timber, plastic waste, cables and remains of fishing nets also occur frequently along the boundary zones.

In 1988 we started a (semi-)quantitative long-term sampling programme of the *Idotea* species associated with surface drift material off Helgoland. Every summer (July to October), a number of samples were taken at irregular intervals depending on weather conditions. Drift material was collected, from aboard a motor boat, using a hand net of 1-mm mesh size. A total of 99 samples were collected during the 11-year period from 1988 to 1998. The sample size varied between about 1 and 20 kg of algal material. The animals were separated quantitatively from the algae by carefully washing the material with seawater.

The samples usually contained a great number (often several thousands) of mancas and young juveniles. However, only specimens with a body length of more than 10 mm (advanced juveniles and adults) were considered for the study because it is only this fraction which can be identified easily to species level. Abundances were expressed in numerical densities (number of individuals per kilogram fresh weight of algae). Additionally, in the summer of 1995, a total of about 1200 sampled *Idotea* specimens with a body length of less than 10 mm (mancas: 3–6 mm; young juveniles: 6–10 mm) were raised in the laboratory until they could be determined easily to species level. One hundred individuals each were kept in plastic cups with 5 l of aerated seawater. The water was changed every 3-4 days. Food (fragments of the brown alga *Ascophyllum nodosum* and freshly hatched *Artemia* nauplii) was available ad libitum.

During a cruise of the Biologische Anstalt Helgoland (BAH) research vessel "Heincke" in September 1995 from Lisbon (Portugal) via Gibraltar to Nice (France), surface drifting material was collected in the western Mediterranean and was examined with respect to associated isopods. Some hundreds of *I. metallica* were isolated from this material and were taken to Helgoland by plane in order to be used in crossing experiments with North Sea specimens. Reciprocal crossings (North Sea males × Mediterranean females, and vice versa) were performed. The F1 generation was tested for fertility by crossing among each other.

Since 1962, on every workday surface water temperatures at Helgoland have been measured along with other hydrographic parameters by the BAH. All calculations of possible changes in temperatures during the 37-year period from 1962 to 1998 are based on this time series.

RESULTS

Surface drift material was found to attract a great variety of macrofaunal species such as fish larvae, decapod larvae, isopods, amphipods and other small crustaceans. The habitat was dominated quantitatively by different species of the isopod genus *Idotea* and by the amphipod *Gammarus locusta*.

All eight species of *Idotea* known from British waters (Naylor, 1972) were also found among drift seaweed off Helgoland (Table 1). The principal isopod inhabitant of drift material was *Idotea baltica*. It was the only species of the genus represented in all 99 samples; furthermore, it was always by far the most abundant of all *Idotea* species, representing 63.9–98.4% (mean: 89.1 ± 7.7%) of the total numbers of individuals of a sample. *I. pelagica*, *I. granulosa*, *I. chelipes*, *I. emarginata*, *I. linearis* and *I. neglecta* do not typically inhabit drift material. These species have divergent specific habitats, yet

Table 1. Results of an 11-year quantitative study of *Idotea* species associated with surface drift material off Helgoland

Year	No. of samples	No. of individuals > 10 mm (total and per kg seaweed)	Total no., no. per kg seaweed, and (in parentheses) % of *I. baltica*	*I. emarginata*	*I. neglecta*	*I. granulosa*	*I. pelagica*	*I. linearis*	*I. chelipes*	*I. metallica*
1988	4	2900	2696	160	28	13	2	0	0	0
		61.3	57.0	3.4	0.6	0.2	0.1	0	0	0
			(93.0)	(5.5)	(1.0)	(0.4)	(0.1)	(0)	(0)	(0)
1989	24	21334	19979	578	173	275	71	127	132	0
		90.9	85.1	2.5	0.7	1.2	0.3	0.5	0.5	0
			(93.6)	(2.7)	(0.8)	(1.3)	(0.3)	(0.6)	(0.6)	(0)
1990	5	3800	3005	309	54	176	37	195	20	0
		50.3	39.8	4.1	0.7	2.3	0.5	2.6	0.3	0
			(79.1)	(8.1)	(1.4)	(4.6)	(1.0)	(5.1)	(0.5)	(0)
1991	2	889	851	10	4	0	0	24	0	0
		39.2	37.5	0.4	0.2	0	0	1.1	0	0
			(95.7)	(1.1)	(0.4)	(0)	(0)	(2.7)	(0)	(0)
1992	8	6355	5253	471	240	72	16	290	13	0
		46.2	38.2	3.4	1.8	0.5	0.1	2.1	0.1	0
			(82.7)	(7.4)	(3.8)	(1.1)	(0.3)	(4.6)	(0.2)	(0)
1993	5	2866	2709	69	40	12	0	36	0	0
		53.5	50.6	1.3	0.7	0.2	0	0.7	0	0
			(94.5)	(2.4)	(1.4)	(0.4)	(0)	(1.3)	(0)	(0)
1994	12	9427	8628	129	160	29	26	403	48	4
		43.1	39.4	0.6	0.7	0.1	0.1	1.9	0.2	0.02
			(91.5)	(1.4)	(1.7)	(0.3)	(0.3)	(4.3)	(0.5)	(0.04)
1995	7	3040	2622	115	84	17	0	129	41	32
		67.0	57.8	2.5	1.9	0.4	0	2.8	0.9	0.7
			(86.3)	(3.8)	(2.8)	(0.6)	(0)	(4.2)	(1.3)	(1.1)
1996	10	6035	5592	90	88	51	11	170	33	0
		36.8	34.1	0.6	0.6	0.3	0.1	1.0	0.2	0
			(92.7)	(1.5)	(1.5)	(0.8)	(0.2)	(2.8)	(0.5)	(0)
1997	5	3613	2704	104	5	28	2	253	517	0
		59.0	44.1	1.7	0.1	0.5	0.1	4.1	8.4	0
			(74.8)	(2.9)	(0.1)	(0.8)	(0.1)	(7.0)	(14.3)	(0)
1998	17	12876	12320	230	141	20	0	0	0	165
		73.3	70.1	1.3	0.8	0.1	0	0	0	1.0
			(95.7)	(1.8)	(1.1)	(0.2)	(0)	(0)	(0)	(1.3)

Table 2. Results of a 6-week rearing experiment designed to determine to species level, 1200 young *Idotea* (< 10 mm in length) collected from drift material off Helgoland in July and August 1995. The experimental animals were raised in 12 groups of 100 individuals each

Running no. of experiment	No. of survivors (out of 100)	Mortality (%)	No. (and %) of *I. baltica*	*I. emarginata*	*I. neglecta*	*I. granulosa*	*I. pelagica*	*I. linearis*	*I. chelipes*	*I. metallica*
1	80	20	72 (90.0)	8 (10.0)	0	0	0	0	0	0
2	75	25	59 (78.7)	11 (14.7)	0	0	0	0	0	5 (6.7)
3	90	10	77 (85.5)	9 (10.0)	2 (2.2)	2 (2.2)	0	0	0	0
4	64	36	46 (71.9)	13 (20.3)	3 (1.6)	0	0	0	0	2 (3.1)
5	83	17	80 (96.4)	1 (1.2)	0	0	0	0	0	2 (2.4)
6	77	23	61 (79.2)	14 (18.2)	2 (2.6)	0	0	0	0	0
7	69	31	55 (79.7)	5 (7.2)	6 (8.7)	0	0	0	3 (4.3)	0
8	85	15	71 (83.5)	7 (8.2)	0	0	0	0	1 (1.2)	6 (7.0)
9	81	19	81 (100)	0	0	0	0	0	0	0
10	88	12	73 (83.0)	10 (11.4)	0	0	0	0	0	5 (5.7)
11	76	24	66 (86.8)	0	7 (9.2)	0	0	0	3 (4.0)	0
12	90	10	85 (94.4)	0	0	0	0	0	0	5 (5.6)
Total	958	79.8	826 (86.2)	78 (8.1)	20 (2.1)	2 (0.2)	0	0	7 (0.7)	25 (2.6)

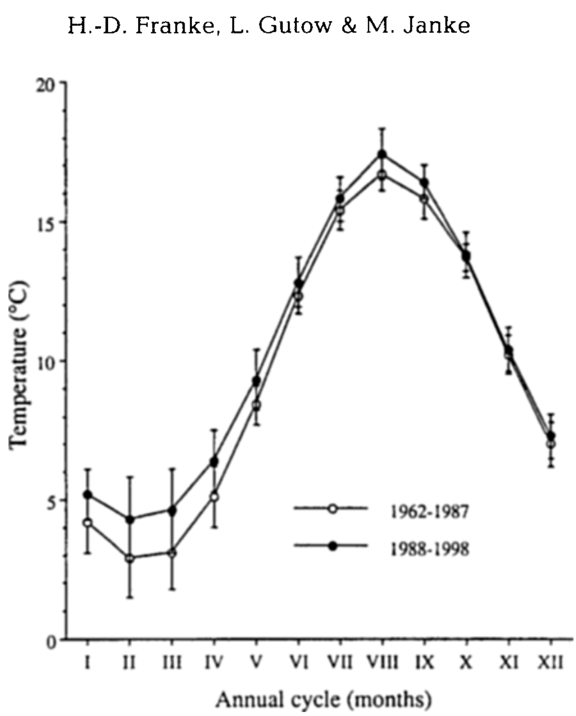

Fig. 1. Annual course of monthly means of surface seawater temperature at Helgoland for the 26-year period 1962–1987 (○) and the recent 11-year period 1988-1998 (●)

may associate occasionally with drift material, using it as a means of passive dispersal (Naylor, 1955; personal observations). In contrast, *I. baltica* and *I. metallica* seem to live predominantly amongst drift seaweed which represents the species' typical habitat in North Atlantic waters (Naylor, 1955, 1957; Holdway & Maddock, 1983; Locke & Corey, 1989).

In the summer of 1994 we recorded, for the first time, a few specimens of *I. metallica*, including one gravid (ovigerous) female. The specimens conformed to the description given by Naylor (1957, 1972). In the summer of 1995, *I. metallica* was again present in the Helgoland region. The number of individuals (per kilogram fresh weight of collected seaweed) was slightly higher than in the previous year. Among the 32 specimens collected were 6 gravid females. This material was used to establish a laboratory mass culture of *I. metallica* (details will be reported elsewhere). Because no samples were collected during the winter of 1994/1995, it is not clear whether the species really overwintered in the German Bight or whether it did not survive the winter conditions and then returned the following year, its presence in the summer of 1994 and 1995 thus representing two independent phases of immigration.

After the severe winter of 1995/1996, the species was completely absent from the samples collected in summer 1996. In the summer of 1997, only five samples were taken, and again no specimens of *I. metallica* were found. In the summer 1998, however, the species reappeared, there now being higher numbers than ever before, indicating that its appearence in 1994 and 1995 was not a unique event.

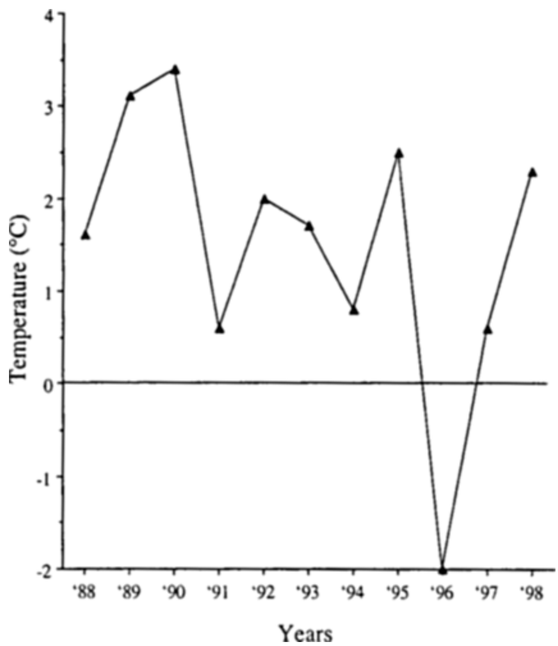

Fig. 2. Lowest monthly means of surface seawater temperature at Helgoland for years 1988–1998, expressed as deviation (in °C) from the long-term average (period 1962–1987) which has been set equal to zero

Mancas and young juveniles collected from drift material in the summer of 1995 were reared successfully in the laboratory. After 6 weeks, the surviving individuals (mortality rate between 10% and 36%, mean: 20.2 ± 8.1%) could be determined easily to species level. In addition to the bulk of individuals which turned out to be *I. baltica*, we recorded individuals of some other *Idotea* species, including a small number of *I. metallica* (Table 2). This indicates that all stages of *I. metallica* were present in the samples, and that the species is able to reproduce successfully in the Helgoland region.

On drift material collected in the western Mediterranean, *I. metallica* was the principal (and usually the only) isopod inhabitant (details will be reported elsewhere). All developmental stages of *I. metallica* were represented in the samples, again indicating that the species undergoes its complete life cycle in association with surface drift material (euneustonic species). *I. baltica* was the only other *Idotea* species which was found, in small numbers, among drift material in the Mediterranean. Crossings between specimens from the Mediterranean and the North Sea were successful, independent of the origin of the male and female partner (reciprocal crossings). The F1 generation proved to be fertile and did not show any obvious difference in fitness compared to the P generation.

From the now available 37-year data series of water temperatures at Helgoland (annual cycles of monthly means), we calculated separate average curves for the 26-year period 1962–1987 and the 11-year period 1988-1998. Monthly means for the period

1988–1998 proved to be consistently higher over the complete annual cycle compared to the period 1962-1987 (Fig. 1). The difference is particularly evident for the winter months, less obvious in spring and summer, and least apparent in autumn. The general warming, i.e. the increase in the annual mean temperature (1962–1987: 9.6 °C; 1988–1998: 10.3 °C), was thus mainly due to an increase in winter temperatures. In 10 out of the 11 years of the recent period 1988–1998, the lowest monthly mean temperature (usually in February, occasionally in January and March, respectively) was above the respective 26-year (1962–1987) long-term average of 2.7 °C (Fig. 2). The only exception was the severe winter of 1996 with a lowest monthly mean (February) of 0.7 °C.

DISCUSSION

From north-west European waters, there have been occasional records of *I. metallica* off the west coast of the British Isles. Naylor (1957) suggested that the species is transported across the Atlantic from North America, occasionally reaching British waters amongst floating objects, carried along by the North Atlantic Drift. Although the species has occasionally been recorded off the west coast of Britain for the past 150 years or so, it "has not so far been able to establish itself as a British resident" (Naylor, 1957). There is no indication of whether this situation has changed since. More recent records from Irish waters have been given by McGrath (1980) and Tully & McGrath (1987).

As to the North Sea, only two chance finds of a single specimen each have been reported for the Norwegian and the Dutch coast, respectively (Pethon, 1970; Huijsman & Huwae, 1978). As far as we know, the species has never been recorded in the German Bight before our first records in the summer of 1994. This is unlikely to simply reflect a lack of diligent examination of samplings: the German Bight (and particularly the Helgoland region) has been an extensively studied marine area for more than a hundred years, and *I. metallica* is a very conspicuous species with respect to habitus and colour. So, if significant numbers of the species were present off Helgoland before 1994, they should certainly have been noticed. Particularly in the period 1988–1993, during the first part of our study, we can definitely exclude the presence of *I. metallica* off Helgoland: among many thousands of *Idotea* individuals which were carefully examined, there was not a single specimen of *I. metallica*.

The origin of the North Sea specimens of *I. metallica* remains open. In our crossing experiments specimens from the Mediterranean and the North Sea were found to be capable of interbreeding, and may thus be recognized as members of the same species. Nevertheless, regarding the hydrographic pattern of the North Atlantic, it seems to be more likely that the North Sea specimens originate from North America and the North Atlantic rather than from the Mediterranean. Only a genetic analysis can provide conclusive evidence.

Considering the species' high natural capacity for dispersal, it appears very unlikely that the arrival of *I. metallica* in the North Sea resulted from an accidental introduction by man. Most likely, we are witnessing an expansion of the range of the species into the North Sea by its natural means of dispersal, as a response to changing environmental conditions. It is hardly a simple coincidence that the first records of *I. metallica* off Helgoland occurred during a summer (1994) that was preceded by a period of mild winters (1989–1994), and that the species was again absent from the area after the severe winter of 1996. The species' reappearance in the summer of 1998 was again preceded by two mild winters. This suggests that some feature related to temperature, probably a lack of extremely low water temperature in winter, is relevant to the observed phenomenon.

There is a growing conviction that global temperatures (including sea surface temperatures) are rising, and that this general warming trend results for the most part from man's activities (Folland et al., 1992; Mitchell et al., 1995; IPCC, 1996). Because of the complexity of the phenomena, however, there is still considerable uncertainty as to the details of the anticipated climate change (extent and speed of change, differences on regional scales).

Parameters connected with environmental temperature are among the most important physical variables controlling the large-scale distributions and the abundances of marine organisms, though it is often not clear what aspects of temperature are the crucial limiting conditions and what their exact mode of action is (Orton, 1920; Hengeveld, 1990; Bhaud et al., 1995). It is not surprising, thus, that in most scenarios the predicted climate change will have profound implications for ecological conditions (e.g. Vitousek, 1994). Rather than by mean temperatures and the range commonly experienced, distributions and abundances of many species are strongly influenced by the extremes of temperature. As to the continentally influenced North Sea, it is winter temperature that is particularly relevant to the composition and functioning of the ecosystem (e.g. Beukema, 1990).

A recent temperature increase in coastal waters of the southern North Sea is evident. Nevertheless, it is presently still impossible to assess whether this is simply a short-term phenomenon similar to phenomena which have already been recorded occasionally in the past, e.g. around 1974 , or whether we are really witnessing the beginning of the predicted long-term warming trend (Becker & Pauli, 1996). No matter how, the responses of populations and ecosystems to periods with mild winters can give us some idea of what might happen in a warmer North Sea (Beukema, 1992). There can be little doubt that a persistent warming trend, particularly a lack of extremely cold winters, will have serious consequences on the structure and functioning of the North Sea ecosystem. A lack of severe winters will favour the large number of North Sea species which are known to be sensitive to low temperatures (Beukema, 1992), and species with a more oceanic (southerly) distribution pattern may be expected to extend their ranges northeastwards into the North Sea (Greve, 1994; Greve et al., 1996). Although there are also species which will probably be negatively affected by a warming trend and might finally even disappear from the area, it has been predicted that species richness in the Wadden Sea (and this may also apply to the North Sea as a whole) may increase rather than decrease in a warmer climate (Beukema, 1990, 1992; de Vooys, 1990).

The oceanic *I. metallica* may be one of the potential immigrants to a warmer North Sea, whether as a regular summer immigrant or even as a permanent resident. A climate shift, however, is only a necessary precondition for the species to extend its geographical range into the North Sea. Whether the species can take full advantage of an altered situation and will really establish itself permanently in the new environment depends on whether it is limited primarily by climatic factors rather than by competitive (and/or other biological) ones. Because of the complexity of the relevant biological interactions, the exact ecological consequences of a climate shift for a particular area are hard to predict.

It is generally known that the arrival of a new element in a particular environment may have a significant, sometimes highly detrimental, impact on an established ecosystem. Dramatic recent examples are the arrival of the alga *Caulerpa taxifolia* in the Mediterranean (e.g. Bellan-Santini et al., 1996), the Ctenophore *Mnemiopsi leidyi* in the Black Sea (e.g. Kideys, 1994), and the zebra mussel *Dreissena polymorpha* in the North American Great Lakes (e.g. Ludyanskiy et al., 1993), to name but a few. In contrast, there are also many cases of newly arrived species which were able to find unexploited resources and thus became assimilated into communities without any obvious impact on the native biota. The responses of *I. metallica* to different temperature regimes as well as the effects which a successfully immigrating *I. metallica* might exert on competing native species (and vice versa) are the subject of current laboratory studies. There is no indication that *I. metallica* might become a key population with a great impact on the North Sea ecosystem; however, the species may serve as a sensible indicator of a possible warming trend in the southern North Sea.

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