

Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa*: indication for extended parental care and advanced social behaviour

M. THIEL*

Smithsonian Marine Station, 5612 Old Dixie Highway, Fort Pierce,
FL 34946, USA

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Leucothoe spinicarpa (Abildgaard, 1789) is an endobiotic amphipod, commonly found in sponges, bivalves and ascidians. I examined the occurrence and population demographics of *L. spinicarpa* in different species of solitary and stolonal ascidians from two lagoonal embayments on the Florida Atlantic Coast. Between 77 and 95% of the solitary ascidians *Ascidia nigra* (Savigny, 1816), *Microcosmos exasperatus* Heller, 1878 and *Styela plicata* (Leseuer, 1825) were hosts to *L. spinicarpa*. The high rate of occupancy in large solitary ascidians by *L. spinicarpa* in September 1997 suggests that competition for these microhabitats can occur. The average number of amphipods ascidian⁻¹ varied between 1.89 ± 0.48 s.e. in *S. plicata* and 5.60 ± 1.24 s.e. in *M. exasperatus* both from the Indian River Lagoon. The maximum number of amphipods ascidian⁻¹ was 30 in *A. nigra* from Lake Worth. Prevalence of *L. spinicarpa* in stolonal ascidians is substantially lower than in solitary ones. Many zooids contained no amphipods, but at one site, 9.4% of all zooids of *Clavelina oblonga* Herdman, 1880 were host to *L. spinicarpa*. At this location, usually single amphipods were found in a zooid, however, one zooid of *C. oblonga* contained three amphipods and another zooid contained four. The size range of *L. spinicarpa* found in solitary ascidians differs considerably from that of amphipods collected in stolonal species. All sizes of amphipods occurred in solitary ascidians, while individuals found in stolonal ascidians were usually < 5 mm and immature. Some solitary ascidians contained an adult male and female pair and a clutch of similar-sized juveniles. These observations show that juveniles remain in their parents' dwelling after hatching from the female's brood pouch. It is concluded that after leaving the parental dwelling, many subadult *L. spinicarpa* seek shelter in the zooids of stolonal ascidians before they relocate to larger, solitary ascidians when reaching maturity. The demographics of amphipod groups suggest that some offspring reach maturity in their parents' dwelling and inherit the parental ascidian after the death of their parents. Thus, in this ascidian-dwelling amphipod extended parental care in a stable microhabitat may have led to the evolution of advanced social behaviour.

KEYWORDS: Amphipoda, ascidians, association, host-specialization, parental care.

*Present address: Facultad de Ciencias del Mar, Universidad Catolica de Norte, Larrondo 1281, Campus Guayacan, Coquimbo, Chile.

Introduction

Several marine isopods and amphipods are known to dwell temporarily or throughout their lives within a variety of host organisms such as sponges, bivalves, brachiopods, sea anemones, ascidians, salps or in hermit crab shells (Vader, 1970a, b, 1971, 1972, 1983, 1984a, b, 1995; Myers, 1974; Heard and Perlmutter, 1977; Richter, 1978; Thomas, 1979, 1997; Laval, 1980; Biernbaum, 1981; Vader and Beehler, 1983; Costello and Myers, 1987; De Broyer and Vader, 1990; Shuster, 1992, 1995; LeCroy, 1995; Vader and Krapp-Schickel, 1996; Vader and Myers, 1996). While the hosts appear to gain little or no advantage, associates living within host organisms find a stable microhabitat that provides shelter from predation and in some cases nutrition. Some amphipod and isopod associates have been characterized as commensals that benefit from their hosts but do not inflict harm on them (Vader and Beehler, 1983; Jaramillo *et al.*, 1981; Vader, 1995), while other associates are viewed as parasites that feed on their host's tissue or affect their host's performance otherwise (Vader, 1985; Moore *et al.*, 1994; Duffy, 1996a). In most cases, however, very little is known about the details of these associations.

An important prerequisite for a detailed study of the above associations is to know about the frequency of their occurrence and the general biology of both the hosts and their associates. Published records of these associations are often based on occasional observations (sometimes years after samples were taken), and in many cases it is impossible to identify how frequently a specific association may have occurred in the field. Studies that specifically examine the frequency of these associations are relatively few (see e.g. Ortiz, 1975; Vader and Krapp-Schickel, 1996; Dalby, 1996), although this knowledge is essential for an understanding of the association. At present, particularly the life histories of many associate species are unknown or are only known in parts. A puzzling example is the case of the amphipod *Onisimus normani* G.O. Sars, 1890 that lives in the gastrovascular cavity of sea anemones as juvenile but disappears from the host just before reaching maturity. Oviparous females of this species have never been found within hosts and are rarely observed elsewhere (Vader, 1967, 1970b; Vader and Lønning, 1973). Although some species, such as the amphipods *Colomastix* spp., *Leucothoe spinicarpa* and *Paraleucothoe novaehollandiae* (Haswell, 1880) are very common as associates of sponges and ascidians from shallow coastal waters (Ortiz, 1975; Heard and Perlmutter, 1977; Biernbaum, 1981; Vader, 1984a,b; Costello and Myers, 1987; LeCroy, 1995; Dalby, 1996), surprisingly little is known about their life history.

Some associates apparently dwell in a variety of host species, while others are very host-specific. Particularly among associates that are host-specific, indications for strong interactions among associates (i.e. colony-members) from one host-individual have been recognized. For example, in the sponge-dwelling isopod *Paracerceis sculpta* (Holmes, 1904) three male morphotypes have been found (Shuster, 1987), two of which are not capable of acquiring a harem (Shuster, 1992, 1995) but gain successful access to mature females by sneaking into established harems (Shuster and Wade, 1991). In the amphipod *Anamixis hanseni* Stebbing, 1897 that lives in zooids of stolonal ascidians two distinctly different male morphs exist (Thomas and Barnard, 1983), and removal of the hyper-male results in the transformation of one of the beta-males to a hyper-male (J.D. Thomas, personal communication). Both these peracarid species are host-specific, having only been found in the sponge *Leucetta losangelensis* (de Laubenfels, 1930) (*P. sculpta*) and in the tunicate *Ecteinascidia turbinata* Herdman, 1880 (*A. hanseni*, see Thomas, 1979).

Similarly, sponge-dwelling synalpheid shrimp species, among which is the first reported eusocial marine invertebrate (see Duffy, 1996b), are very host-specific (Duffy, 1996a). The host-specialization of crustacean associates such as *P. sculpta*, *A. hanseni* and synalpheid shrimp species may potentially result in hosts becoming a limited resource. Strong intraspecific competition for these hosts (= breeding habitats) may prevent some individuals from successfully acquiring a harem, i.e. the competitively inferior males in *P. sculpta* (Shuster, 1987), or excluding them from reproduction altogether such as the non-breeding individuals in *Synalpheus regalis* Duffy, 1996 (Duffy, 1996b). Thus, host-specialization may have important consequences for the reproductive biology of these associates. Many other associates, however, show only little host-specialization. For example, *Colomastix janiceae* Heard and Perlmutter, 1977 has been reported from a variety of sponge species (LeCroy, 1995), and *L. spinicarpa* has been reported from a variety of sponges and ascidians (Ortiz, 1975; Vader, 1984a, b; Costello and Myers, 1987). These 'generalist' associates may not be faced with intraspecific competition for hosts or mates to the same degree as the above-mentioned host-specific crustaceans. Competitively inferior individuals of generalist associates may simply search for alternative hosts. The occurrence of non-reproductive individuals is therefore less likely in generalist than in host-specific associates.

In this study, I examined whether *L. spinicarpa* is indeed a generalist associate of sponges and ascidians, as indicated by several previous studies (Ortiz, 1975; Biernbaum, 1981; Costello and Myers, 1987). Herein, I ignored sponges as amphipod habitats but rather focused on ascidians as potential hosts to *L. spinicarpa* for several reasons. Sponges and ascidians differ considerably morphologically and functionally. In sponges, amphipods inhabit the spongocoel in which water has been efficiently filtered by the sponge before it reaches the associate. In ascidians, the amphipods are usually found in the branchial chambers (Harant, 1931; Monniot, 1965; Millar, 1971) where they encounter incoming water before it is filtered by the host. In the study area, various solitary and stolonal ascidian species can be found, so that the host use pattern of *L. spinicarpa* can be examined without the danger of confounding the results by substantial functional differences of potential hosts. Despite considerable differences in shape and size, all ascidians examined in this study feature a distinct branchial chamber with one inhalant and one exhalant opening, thereby maintaining a basic morphology and flow-through regime. Another reason for limiting this study to ascidians as potential hosts is the fact that under the species name *Leucothoe spinicarpa* probably several cryptic species occur along the coasts of southern Florida (Thomas, 1993). At least two (possibly three) distinctly different colour morphs of *L. spinicarpa* are found in the study area, one of which has been previously identified and reported from ascidians (Ortiz, 1975). This latter colour morph has a brownish back (Ortiz, 1975, figure 5), and is the focus of the present study. It can be easily distinguished from a completely white colour morph that is frequently found in sponges in the Indian River Lagoon (personal observation).

Two objectives were pursued in this study: 1) to examine the host use pattern of *L. spinicarpa*, and 2) to examine the population demographics of *L. spinicarpa*. In combination, these data provide basic information on the life history of these ascidian-dwelling amphipods.

Material and methods

Ascidians were collected between 17 and 30 September 1997 along the Atlantic Coast of Florida at three different sites in the Indian River Lagoon (Little Jim's—

27°28'40"N, 80°18'45"W; Fort Pierce Inlet—27°28'05"N, 80°17'50"W; Fort Pierce City Marina—27°26'55"N, 80°19'20"W) and at Lake Worth (26°47'01"N, 80°02'35"W). Water temperatures at the collection sites vary according to the tidal stage, season and rainfall between about 15°C in the winter months and 30°C in the summer months (Gilmore, 1977). Salinities vary between 16 and 36ppt. All ascidians were collected at about 0.1–1 m below Mean Low Water from artificial structures such as ropes, boat ramps, pilings or floating docks. Individual ascidians or colonies were carefully separated from their substrata, gently cleaned from fouling organisms and immediately placed in individual plastic containers. Upon arrival in the laboratory, solitary ascidians were carefully dissected and examined for amphipods. The dry weight of solitary ascidians was determined after drying them for 24 h at 70°C. Individual zooids of stolonal ascidians were examined for the presence of amphipod associates by either visual observation (in the translucent *Clavelina oblonga*) or dissection of zooids (*Ecteinascidia turbinata*, *Polyandrocarpa zorritensis* (Van Name, 1939) and *Ecteinascidia tortugensis* Plough and Jones, 1939). Occasionally, the behaviour of *L. spinicarpa* in its host was observed through a dissecting microscope before dissecting the ascidians.

All amphipods were preserved in 5% formalin, later transferred to 70% ethanol and measured along their dorsal surface from the rostrum to the telson with the aid of a computerized video-image analysis-system. In order to identify the sex of the amphipods, they were examined for oostegites. Some amphipods < 4.0 mm had already developed tiny oostegites, but the presence/absence of oostegites was only used to determine the sex of individuals ≥ 4.0 mm. The number of embryos in undisturbed brood pouches was counted. Notes on the position of the amphipods within their hosts made during dissection of ascidians are also provided.

Results

Occurrence of Leucothoe spinicarpa in solitary and colonial ascidians

The amphipod *Leucothoe spinicarpa* is very common in ascidians of the study area. *Leucothoe spinicarpa* was the only macroscopic associate of solitary ascidians, with the exception of one ascidian, *Styela plicata*, from Lake Worth which hosted an ascidicolous copepod. All amphipods collected in the present study belong to the colour morph with the brownish back as described by Ortiz (1975).

About 90% of all *Ascidia nigra* and 77% of all *Styela plicata* from Lake Worth harboured *L. spinicarpa* (figure 1). 95% of all *Microcosmos exasperatus* and 89% of all *S. plicata* from the Indian River Lagoon were hosts to *L. spinicarpa*. The size of the ascidian did not appear to affect its potential as a host for *L. spinicarpa*. When pooling all solitary ascidians, no significant relationship between host size (expressed as dry weight) and the number of associates was found (t-test, $p > 0.05$; figure 2). Thus, all solitary ascidians examined in this study appear equally suitable to be colonized by *L. spinicarpa*, regardless of species and size. The mean number of amphipods ascidian⁻¹ varied between 1.89 ± 0.48 s.e. in *S. plicata* and 5.60 ± 1.24 s.e. in *M. exasperatus*, both from the Indian River Lagoon (figure 3). The maximum number of *L. spinicarpa* found in one solitary ascidian was 30 amphipods in one *A. nigra* from Lake Worth.

Amphipods occurred less frequently in stolonal ascidians. The highest percentage of zooids with amphipods was found in *Clavelina oblonga*, but at one site no amphipods were found in 447 zooids *C. oblonga* examined (figure 1). Only one

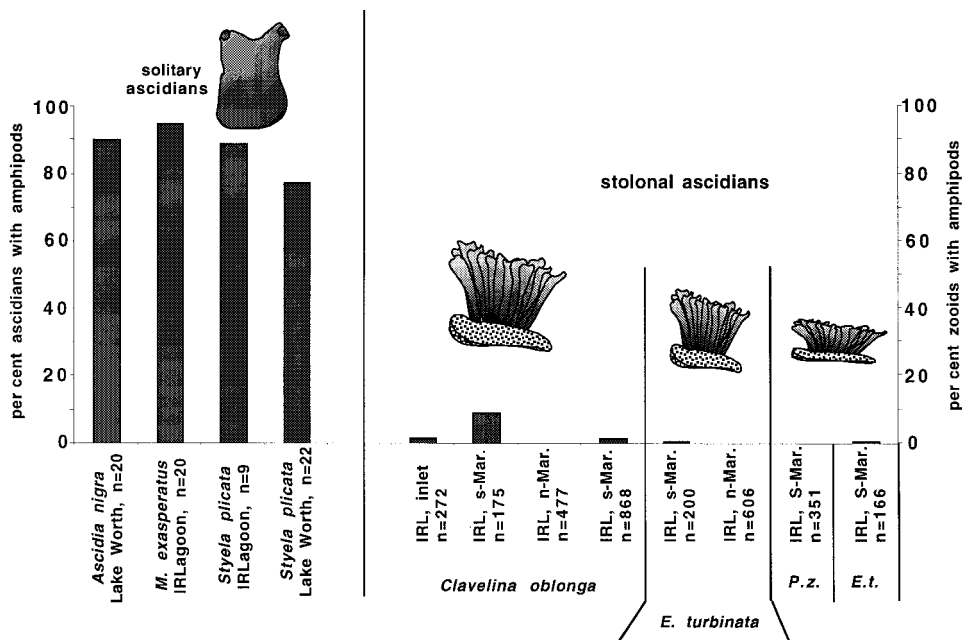


FIG. 1. Per cent ascidians with amphipods *Leucothoe spinicarpa*; percentage of individuals (solitary ascidians) or zooids (stolonal ascidians) with amphipods is shown; n = number of individuals (solitary ascidians) or zooids (stolonal ascidians) examined; *M. exasperatus*—*Microcosmos exasperatus*, *E. turbinata*—*Ecteinascidia turbinata*, *P.z.*—*Polyandrocarpa zorritensis*, *E.t.*—*Ecteinascidia tortuensis*.

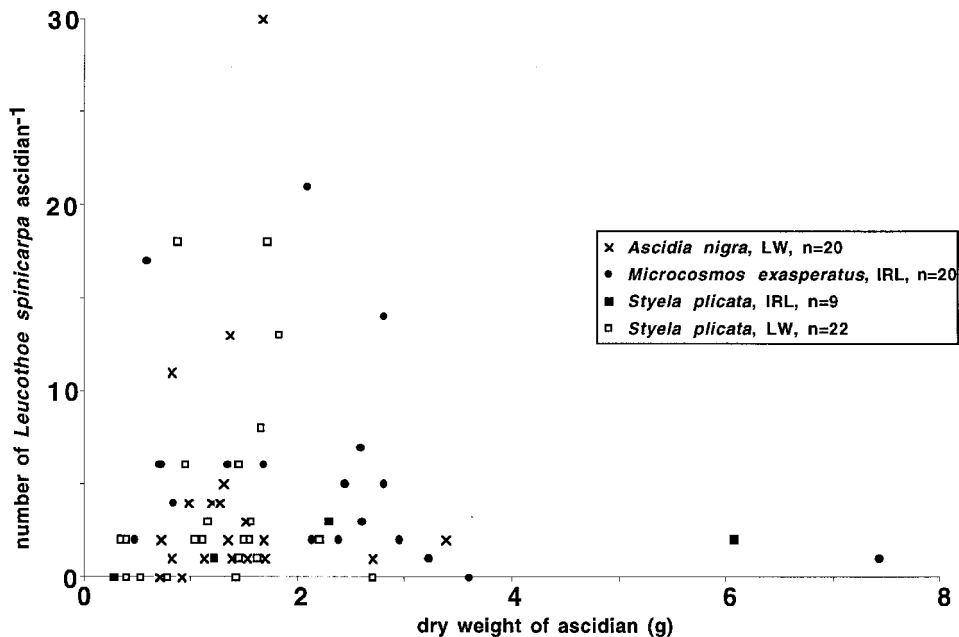


FIG. 2. Relationship between number of *Leucothoe spinicarpa* ascidian⁻¹ and dry weight of ascidians.

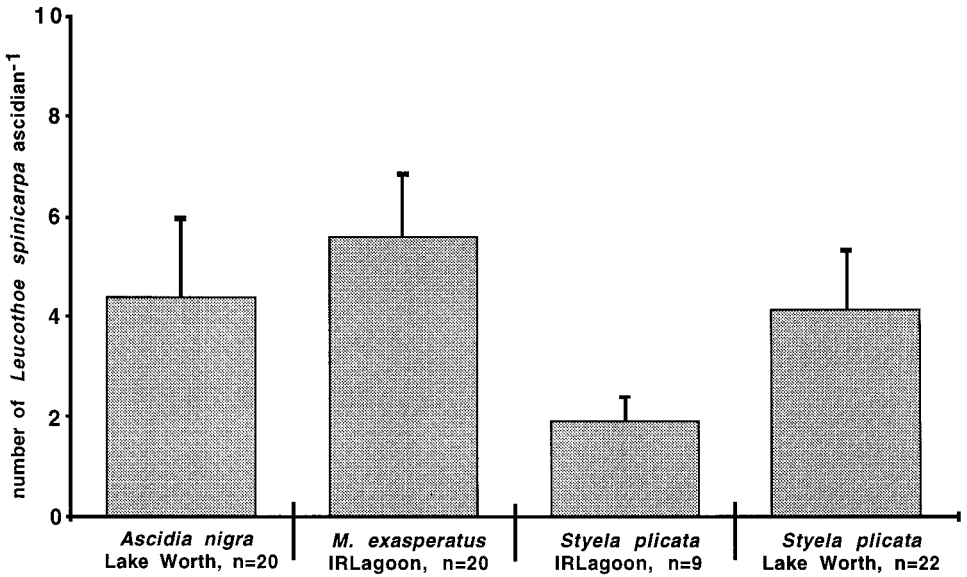


FIG. 3 Mean number \pm s.e. of *Leucothoe spinicarpa* ascidian⁻¹ in solitary ascidians; n = number of ascidians examined.

amphipod each was found in zooids from *Ecteinascidia turbinata* and *E. tortugensis*, and no amphipods were found in *Polyandrocarpa zorritensis*. Thus, amphipods can be found in a variety of stolonal ascidians, but apparently show a preference for the species with the largest individual zooids, *C. oblonga*.

Position of Leucothoe spinicarpa in the ascidian host

All amphipods from *Microcosmos exasperatus* and *Styela plicata* were collected from the inhalant opening. In *Ascidia nigra*, a few amphipods were found in the branchial chamber but most of them were also located in the inhalant opening. When the ascidians closed up, the amphipods were sealed within their hosts. In actively filtering ascidians, the amphipods were observed in the inhalant opening approximately 5–10 mm inside the ascidian with their head orientated towards the exterior. The amphipods remained in this position motionless for at least 5 min and apparently did not change their position when the ascidian closed up temporarily. Similarly, in stolonal ascidians, the amphipods were usually 'wedged' into the inhalant opening, but were occasionally sitting deeper in the branchial chamber or sometimes even in the exhalant opening of the zooid.

Population demographics of Leucothoe spinicarpa in ascidians

Solitary ascidians contained all sizes of amphipods, while zooids from stolonal ascidians only hosted amphipods < 5.0 mm (figure 4). Fifty-nine out of 71 solitary ascidians contained at least one mature *L. spinicarpa*, while 12 ascidians either were empty ($n=9$) or hosted only immature amphipods ($n=3$) (table 1). Of the 59 ascidians containing one or more adult amphipods, 22 were occupied by only females ($n=16$) or males ($n=6$), while the remaining 37 ascidians were jointly occupied by amphipods of both sexes. Two individual ascidians contained seven adult amphipods (see A-17 and B-11 in figure 4). Of all 71 solitary ascidians examined, 18 contained

Table 1. Number of solitary ascidians without and with mature *Leucothoe spinicarpa*.

ascidians with	
no. mature inds.	12
female(s) only	16
males(s) only	6
female(s)+male(s)	37
total	71

no adult females, 40 contained one female and 13 contained two or more adult females (table 2). In the latter 13 ascidians with ≥ 2 adult females, there was maximally one reproductive female (i.e. with embryos in the brood pouch) in each ascidian. Only 26 of all 73 adult females were reproductive. Females contained on average 31.45 ± 2.85 s.e. embryos in their brood pouch ($n=11$ females with undisturbed brood pouches). In several ascidians, clutches of small juvenile amphipods occurred together with one or two large adults (assumed to be the parents) (see e.g. ascidians A-4, A-8, A-17, B-16, B-19, B-21, C-2, C-10, D-13 and D-17 in figure 4).

Discussion

Leucothoe spinicarpa that dwell in solitary and stolonal ascidians are not very host-specific. Adults are found primarily in solitary ascidians while many individuals < 5.0 mm inhabited zooids of the stolonal ascidian *Clavelina oblonga*. The reasons for this apparent ontogenetic change in host-selection will be discussed below.

Host use in Leucothoe spinicarpa and other endobiotic crustaceans

Various host attributes, such as body size, cavity size, filtering activity, or behaviour may affect host selection of associates. Several associate species have been identified as very host-specific from empirical data including the amphipods *Anamixis hansenii* (Thomas and Barnard, 1983) and *Orchomenella recondita* (Stasek, 1958) (De Broyer and Vader, 1983), the isopod *Edotea magellanica* Cunningham, 1871 (Gonzalez and Jaramillo, 1991) and synalpheid shrimp (Duffy, 1996a), but nothing is known about the factors that attract these associates to their specific hosts. Shuster (1992) demonstrated that the osculum diameter of artificial sponges is an important factor affecting their attractiveness to male *Paracerceis sculpta*. In this species, the sponge primarily represents a breeding habitat to which males recruit mature females which they guard and protect within the sponges (Shuster, 1987). Soon after reproduction, the females die and their offspring leave the sponges to feed on algae elsewhere. Apparently, in the amphipod *Onisimus normani* the sea anemone host is a juvenile habitat, but not

Table 2. Number of solitary ascidians with no, 1, 2, 3 or 4 female *Leucothoe spinicarpa*.

ascidians with	
no females	18
1 female	40
2 females	8
3 females	3
4 females	2
total	71

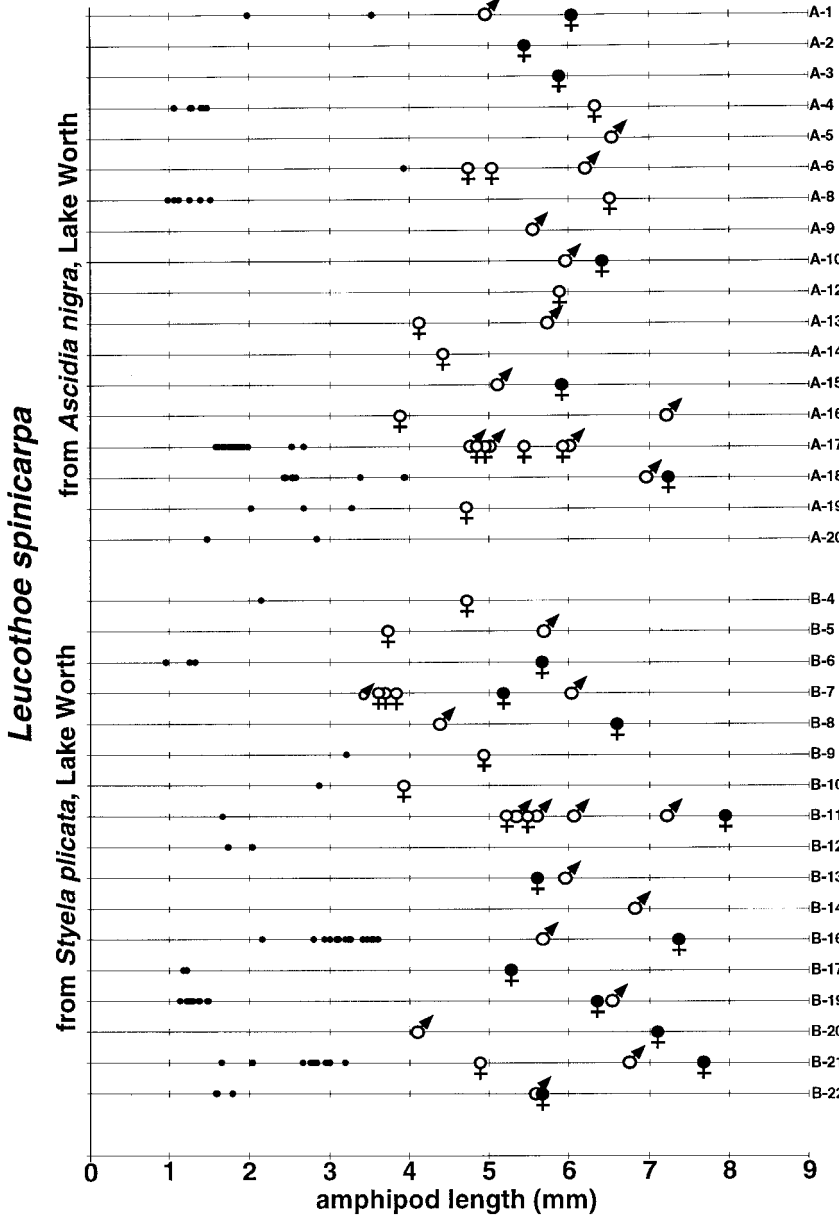


FIG. 4 Sizes of *Leucothoe spincarpa* in solitary and stolonal ascidians; numbers A-1 to F-24 represent all solitary ascidians containing amphipods; symbols represent amphipods within ascidians: dots—immatures; male symbol—mature males, open female symbol—mature females with empty brood pouch, filled female symbol—mature ovigerous females; open squares—immatures from stolonal ascidians; squares with female symbol—immature females; all amphipods from zooids of stolonal ascidians collected at one sampling site and date were pooled.

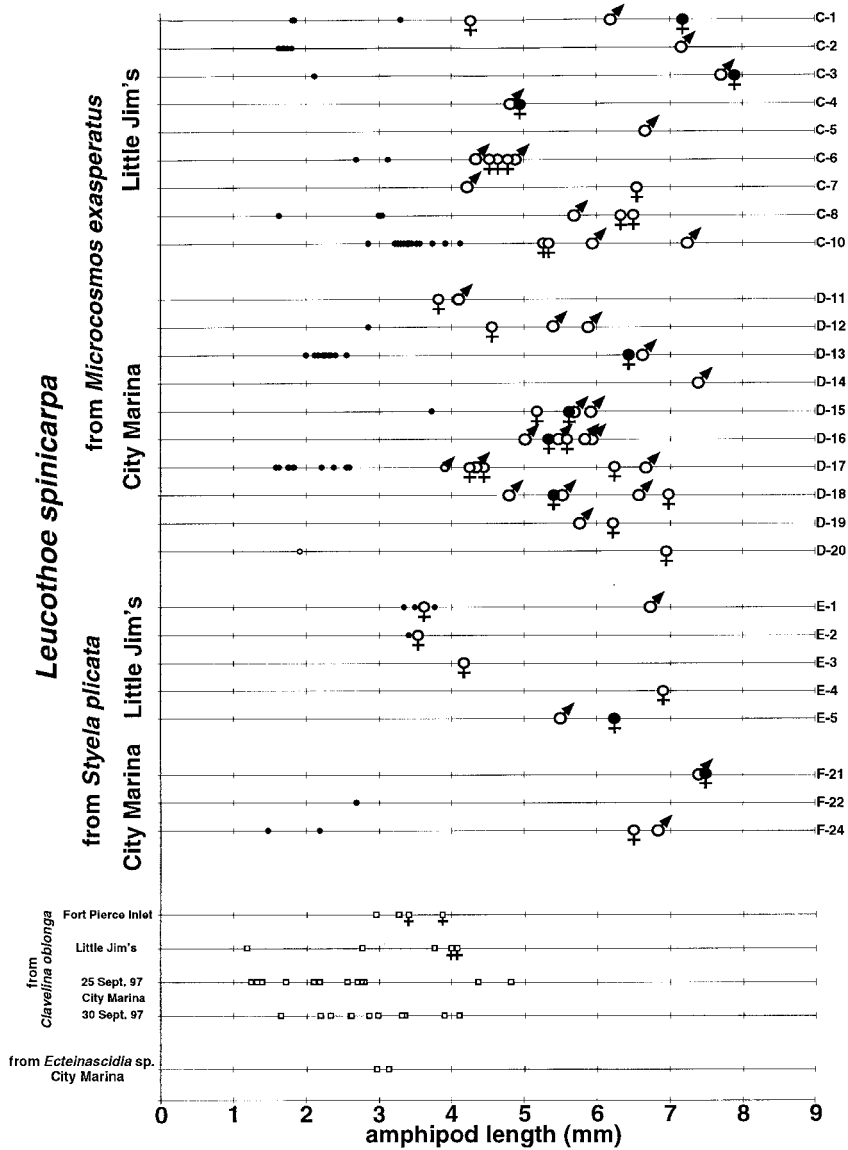


FIG. 4 (Continued)

a breeding habitat, since ovigerous females were never found within sea anemones (Vader, 1967, 1970b). These examples show that some associates do not spend their entire life within a host, but only certain periods. Other associate species, however, spend most of their lives within the host, and necessarily feed either on their hosts or on material available within their hosts. To these latter associates belong many amphipod species such as *Anamixis* spp., *Colomastix* spp. and *L. spinicarpa*, the isopod *E. magellanica* and many synalpheid shrimp species. In comparison to *P. sculpta*, *A. hanseni*, *E. magellanica* and synalpheid shrimp, *L. spinicarpa* is not very host-specific, yet adult *L. spinicarpa* appear to prefer large solitary ascidians. At the time of sampling, almost all solitary ascidians were occupied by adult *L. spinicarpa*, indicating the possibility that competition for this resource exists.

Solitary ascidians may live for several years (Millar, 1971; Svane and Lundäly, 1981, 1982; Svane, 1983; Svane and Young, 1989), and thus constitute a stable micro-habitat suitable for reproductive *L. spinicarpa*. In contrast to the long-living solitary ascidians, individual zooids of stolonal ascidians may grow, reproduce and disappear within weeks to months (see e.g. observations by Davis, 1988; Bingham and Young, 1995). Therefore they are of little value for reproductive *L. spinicarpa*. Furthermore, adults barely fit into even the largest zooids of *Clavelina oblonga*. Stolonal ascidians may thus only constitute a suboptimal habitat for *L. spinicarpa*, but they may be a valuable alternative for juvenile and subadult amphipods when most solitary ascidians are already occupied by adult amphipods. Therefore, I hypothesize that the low host-specialization by *L. spinicarpa* enables subadults of this endobiotic amphipod to avoid intraspecific aggression by seeking alternative habitats. In host-specific associates such as *P. sculpta*, *A. hanseni* and synalpheid shrimp, subadults may be forced to seek shelter or potential mates in habitats already inhabited by adults thereby exposing them to strong intraspecific aggression.

The host-use pattern of *L. spinicarpa* indicates that solitary ascidians represent an important reproductive habitat for this associate species. Among the most important factors attracting the amphipods to these solitary ascidians probably is their size, their strong feeding currents and their longevity. The demographics of the group members cohabiting within individual ascidians indicate that these hosts serve as reproductive habitats for *L. spinicarpa*, similar to bivalves for some isopods and amphipods (Vader and Beehler, 1983; Gonzalez and Jaramillo, 1991). The comparatively small zooids of stolonal ascidians constitute an important habitat for juvenile and subadult *L. spinicarpa*. The immature amphipods are probably vagile, seeking habitat in different host individuals before reaching maturity. During examination of stolonal ascidians, juveniles sometimes left their host-zooids upon slight disturbance (personal observation), further indicating their vagile life style. When reaching adult size, *L. spinicarpa* seek out large solitary ascidians in which they reproduce, as is indicated by the occurrence of one or two large adults and a clutch of small juveniles. As different parts of the population of *L. spinicarpa* inhabit different hosts, this species can temporarily also be expected outside their hosts. Indeed, *L. spinicarpa* has been collected without their respective host (e.g. Ortiz, 1975). However, many of these reportedly 'host-less' specimens may have been dislodged from their hosts as a sampling artifact e.g. in dredge samples.

Extended parental care in Leucothoe spinicarpa and other associates

Juvenile *L. spinicarpa* are at least for a certain time period tolerated by their parents within the parental dwelling as shown by the occurrence of juvenile clutches together with adult amphipods, the latter most likely being the parents.

By engaging in this extended parental care, parents allow their young offspring to find protection during an early phase in their lives, when many benthic invertebrates are particularly susceptible to predation. This form of extended parental care is likely to be found in many other endobiotic marine invertebrates as indicated by some reports on amphipod associates. Observations by Vader (1995) and size distributions provided by Vader and Beehler (1983) strongly suggest extended parental care in other associate species. Juveniles of *Liljeborgia aequabilis* Stebbing, 1888 were sometimes found together with their parents in one hermit crab shell (Vader, 1995), and one or two large individuals of *Metopa glacialis* Krøyer, 1842 were occasionally collected together with 10 to >20 small juveniles within one host individual (Vader and Beehler, 1983, table 1). Several other amphipods such as *Orchomenella recondita* and *Aristias neglectus* Stebbing, 1888 are likely candidates for extended parental care as initial observations have indicated (W. Vader, personal communication). In several sponge-dwelling synalpheid shrimp species, juveniles also remain and develop in the parental dwelling, at least temporarily (Dobkin, 1969; Duffy, 1996b).

Bivalves, brachiopods, sponges and solitary ascidians constitute relatively long-living (several months up to years) host microhabitats ideally suited for the occurrence of extended parental care among associates. Many of these hosts, however reach a maximum size that may not allow for the coexistence of several subadults or adults within one host individual. Thus, growing juveniles have to leave the parental host at some point, and subsequently need to locate a new host. Depending on the host-specialization, juveniles may during this time be able to maintain their reproductive chances (by seeking alternative hosts) or lose them when being forced into intraspecific encounters (when no unoccupied alternative hosts are available). After leaving their parents, some juvenile *L. spinicarpa* maintain their option for a suitable breeding habitat and successful reproduction by avoiding intraspecific encounters and dwelling in the comparatively small zooids of stolonal ascidians.

Some juveniles remain for long time periods in their parents' hosts as indicated by the presence of clutches of relatively large juveniles (see e.g. ascidians A-18, B-18, B-21, C-10, D-13 in figure 4). There does not appear to be a distinct maximal size at which all juveniles leave (or are expelled from) their parents' host. Some juveniles may even reach sexual maturity while still living together with their parents (see e.g. mature amphipods of 3–6 mm size in ascidians B-7, B-11 and D-17 in figure 4). Solely based on population demographics, it cannot be said with certainty that these mature individuals indeed represent offspring of one parental pair. Yet, the fact that they are of very similar sizes and that there are some clutches of very large juveniles (e.g. in ascidian C-10) provide support for this hypothesis. Thus, parents and mature offspring may live together in the same ascidian, potentially resulting in distinct social interactions among these group members. It is not clear at this point whether parents and their maturing offspring compete or cooperate within the ascidians. As during the time when the samples were taken (September), solitary ascidians appeared to be a limiting resource, it may be possible that towards the end of their life parents allow some of their offspring to mature within the parental host. While parents may thus 'bequeath' a valuable reproductive habitat to some of their offspring, they may suppress reproduction of maturing offspring as long as they themselves remain reproductive—there may be up to four mature females in one ascidian, but there is maximally one reproductive female (figure 4). The above arguments indicate that in the ascidian-dwelling amphipod *L. spinicarpa*,

extended parental care may result in advanced social interactions between parents and some of their offspring. Future molecular and experimental studies are required to verify that group members are closely related to each other and to examine how they interact within the limited space of their ascidian host.

Regardless of the familial relationships and the behavioural interactions of the group members, it has been shown in this study that several sexually mature amphipods *L. spinicarpa* may cohabit within one ascidian. While these cohabiting amphipods may not display eusocial behaviour such as the sponge-dwelling *Synalpheus regalis* (Duffy, 1996b), they nevertheless engage in extended parental care and possibly more advanced social behaviour.

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