

# Ecology and natural history of the protochordates<sup>1</sup>

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**Abstract:** The last comprehensive reviews of ecology and natural history of ascidians were included in the excellent 1971 publication by Millar on the biology of ascidians and the 1991 treatise on New Caledonia ascidians by Monniot, Monniot, and Laboute. Several hundred papers have been published since that time, greatly expanding our knowledge of environmental tolerances and responses to increasing levels of anthropogenically derived toxins in marine waters, energetics and feeding strategies, predator–prey relationships, competition both intra- and inter-specific that include many studies of self–nonself recognition in colonial species, modes and environmental regulation of reproduction and development, symbionts, natural-product chemistry as antifouling and antipredator defenses, and dispersal mechanisms. The relatively new field of molecular genetics is revealing the presence of cryptic species and is helping to determine the origin of anthropogenically transported individuals, an important and growing problem that affects natural ecological relationships in marine communities worldwide. We are learning more about the difficult-to-study abyssal and Antarctic species. There have been great advances in our understanding of the importance in open-ocean food webs of the planktonic Appendicularia and Thaliacea. Also included in this review is a brief discussion of recent work on the Cephalochordata and Hemichordata.

**Résumé :** La dernière rétrospective importante sur l'écologie et l'histoire naturelle des ascidies remonte à l'excellente publication de 1971 de Millar sur la biologie des ascidies et à la monographie de 1991 sur les ascidies de la Nouvelle-Calédonie de Monniot, Monniot et Laboute. Plusieurs centaines d'articles ont paru depuis lors, ajoutant aux connaissances sur les tolérances environnementales et les réactions aux concentrations croissantes de toxines d'origine anthropique dans les eaux marines, sur les relations énergétiques et les stratégies alimentaires, sur les relations prédateurs–proies, sur la compétition intraspécifique et interspécifique, en particulier, dans plusieurs études sur l'identification de soi et d'autrui chez les espèces coloniales, sur les modes de reproduction et de développement et leur régulation, sur les symbiotes, sur la chimie des produits naturels utilisés comme moyens de défense et de prévention de l'entassement et sur les mécanismes de dispersion. Le domaine relativement nouveau de la génétique moléculaire révèle l'existence d'espèces cachées et contribue à l'identification de l'origine d'individus transportés par l'activité humaine, un problème important et de plus en plus fréquent qui affecte les relations écologiques naturelles dans les communautés marines à l'échelle globale. Les connaissances s'accroissent sur les espèces abyssales et antarctiques qui sont difficiles à étudier. Le rôle des appendiculaires et des thaliacés planctoniques dans les réseaux alimentaires planctoniques de la haute mer est maintenant beaucoup mieux connu. Les travaux récents sur les céphalochordés et les hémichordés font aussi l'objet d'une courte discussion.

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## Introduction

Aristotle and Pliny were perhaps the first naturalists to leave a written record of their observations. During the 18th

and early 19th centuries leading up to the major voyages of discovery, there was great interest in the natural history of marine animals. In Europe amateur naturalists combed the seashore, and the wealthier ones subscribed to handsomely illustrated magazines detailing the variety of marine life, including a number of ascidians. Scientific taxonomic publications almost always included notes on depth, substrate, and associated fauna and flora. Until the mid-19th century it was believed that no life existed below about 550 m. Each subsequent collecting expedition brought up numerous unknown species including Tunicata and extended the depth at which life could thrive, culminating with the 1872–1876 voyage of the H.M.S. *Challenger* during which ascidians were collected down to about 5350 m (Herdman 1882). Not until the 20th century were serious ecological studies undertaken, beginning with compilations of published observations gleaned from expedition reports and taxonomic treatises and later by

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new work. Abbott (1957) provided an annotated bibliography of literature with ecological content up to that time, as did Berner (1957), for the pelagic tunicates. Much valuable information in Thompson (1930, 1931, 1932, 1934), Berrill (1950), Dybern (1969), and many other papers was included as part of the extensive review covering all aspects of the biology of ascidians by Millar (1971), now over 30 years old but surprisingly still the most recent thorough review of ascidian ecology. Other sources include representatives of the Tunicata as part of more general studies on invertebrates (MacGinitie and MacGinitie 1949; Abbott and Newberry 1980; Kozloff 1990; Ruppert and Barnes 1994). Monniot et al. (1991) superbly summarized major aspects of ascidian ecology and natural history along with a comprehensive overview of morphology and systematics of all ascidian families and genera. Much relevant information can be found in the many diverse papers in Sawada et al. (2001).

This review primarily covers the Chordata subphylum Tunicata, class Ascidiacea, including recent research on abyssal species. This is followed by a shorter section on the Appendicularia and Thaliacea, since these planktonic classes were admirably covered in Bone (1998), and a discussion of the subphylum Cephalochordata. The review concludes with the hemichordates, because it is a group traditionally included with the protochordates, although recent molecular studies by Cameron (2005), Zeng and Swalla (2005), and others in this issue show that they are not closely allied. In attempting to cover the several hundred relevant papers that have been published since 1971, wherever possible I have emphasized reviews or an author's most recent papers on particular topics or groups to keep the reference section to a manageable size.

The protochordates are exclusively marine, occurring worldwide in all oceans. The Tunicata comprise the largest group, recorded from the Arctic to the Antarctic and from the surface to the deepest abyssal regions (Monniot et al. 1991). There are approximately 2800–3000 species of ascidians, 20–25 sorberaceans (see below for a discussion of this controversial abyssal group), 75 appendicularians, and 85 thaliaceans. The subphylum Cephalochordata comprises about 30 species and the phylum Hemichordata comprises about 100 species.

## Phylum Chordata, subphylum Tunicata

### Class Ascidiacea

#### *Environmental tolerances*

The environmental variables most important in determining ascidian distribution (not including anthropogenic transport) are temperature (Brunetti et al. 1985; Marin et al. 1987; Nomaguchi et al. 1997), salinity (Sims 1984; Toop and Wheatly 1993; Vázquez and Young 1996, 2000), light (Lambert and Brandt 1967; Olson 1983; Young and Chia 1984; Durante 1991; Forward et al. 2000; Tsuda et al. 2003), and hydrodynamics (Young and Braithwaite 1980; Havenhand and Svane 1991; Holloway and Connell 2002). There is in general a tolerance to a wider range of temperatures than salinities, with few species surviving below 25‰. Ocean warming during El Niño conditions, and the more gradual global warming that is occurring, has been an important fac-

tor in changing species assemblages over time and in facilitating the successful introduction of nonindigenous species (Stachowicz et al. 2002b; Lambert and Lambert 1998, 2003). Very few ascidians can tolerate any dessication and thus nearly all are below low-tide level (Young 1989). Relatively few species live in areas of heavy wave action, with most preferring at least somewhat protected areas but with good water movement (Abbott and Newberry 1980; Carballo 2000; Goodbody 2000). Floating eggs and embryos of some species have protective mechanisms against UV radiation (Epel et al. 1999), as may the heavily pigmented tunic of *Phallusia nigra* Savigny, 1816 (Hirose 1999). UV exposure has been shown to be highly damaging to the floating eggs and embryos of *Corella inflata* Huntsman, 1912 (Bingham and Reitzel 2000), but the embryos are protected by being retained in the parental brood chamber, as well as the selection of shaded locations by the larvae for settlement. The tunic bladder cells of *Lissoclinum patella* (Gottschaldt, 1898) protect its photosynthetic symbiont *Prochloron* (ex Lewin, 1977) from UV damage (Dionisio-Sese et al. 2001; Maruyama et al. 2003). In this issue, Bates (2005) has a more detailed review of protective mechanisms against UV damage, especially of eggs and embryos.

A number of species, especially those most abundant in polluted harbors, can tolerate and accumulate as adults heavy metals such as arsenic, cadmium, chromium, cobalt, copper, iron, lead, mercury, selenium, tin (as tributyltin), and zinc (Papadopoulou and Kaniyas 1977; Philp et al. 2003). All of these metals, but especially tributyltin, have dose-dependent toxic effects on the development of embryos and larvae (Cima et al. 1996; Bellas et al. 2001; Beiras et al. 2003) and on many enzyme functions including those involved in the immune response (Tujula et al. 2001; Cima et al. 2002; Azumi et al. 2004; Cima and Ballarin 2004). This has led to the use of certain species in bioassays for pollutants (Monniot et al. 1986). Genes controlling the production of heat shock proteins (hsp) may be triggered to turn on by environmental stresses. Agell et al. (2004) showed that pollutants such as copper can induce hsp production in the Mediterranean ascidian *Pseudodistoma crucigaster* Gaill, 1972, which may be useful "as an early warning system for sublethal pollution but that the response is inhibited above a threshold of the stressing agent". Bates (2005) covers the importance of hsp during early development and metamorphosis.

Most native species are very sensitive to pollution and eutrophication from anthropogenic activities and usually decline in abundance and diversity (Naranjo et al. 1996; Goodbody 1993). However, when environmental conditions improve, many species can quickly rebound (Rees et al. 2001).

#### *Dispersal by natural and anthropogenic means*

Because adult ascidians are sessile, all natural dispersal takes place at the gamete and larval stages in free-spawning species or at the tadpole stage for brooding species, although a few colonial species can migrate slowly over small distances (Birkeland et al. 1981; Olson 1983). Marshall et al. (2002) found that in the free-spawning *Pyura stolonifera* (Heller, 1878) (actually *Pyura praeputialis* (Heller, 1878); see Castilla et al. 2002), egg size varies within the same in-

dividual, with larger eggs having higher fertilization success at low sperm concentration and vice versa for smaller eggs. This species occurs in dense mats in Australia, and when spawning occurs there will be a large variation in sperm concentration, thus favoring the maintenance of a heterogeneous egg size distribution and subsequent variation in larval and postlarval size. Much attention has been directed to the dispersal capabilities and substrate selection of the short-lived nonfeeding larvae (Jackson 1986; Svane and Young 1989 for review; Bingham and Young 1991; Goodbody 1995; Young 1995; Marshall and Keough 2003). Most require a hard substrate, a few such as some molgulids anchor in mud or sand with hairlike tunic protrusions, and a few are interstitial (Monniot 1986). The stalked Antarctic colonial ascidian *Distaplia cylindrica* (Lesson, 1830), which may reach a height of 7 m, anchors to soft substrates by a bulbous base (McClintock et al. 2004). Numerous studies have shown that after becoming competent to settle the tadpoles can delay settlement for many hours and even days in the absence of appropriate cues (Svane and Young 1989; Havenhand 1991), which is a strategy that would theoretically increase dispersal distance. However, recent studies show that too long a delay leads to drastic declines in energy reserves, resulting in lowered postlarval size, growth rate, and survivorship (Marshall and Keough 2003). Thus, the hypothesis that introductions might be the result of larval survival in ship ballast water for several days (G. Lambert 2001) may apply to only a few species. Under natural conditions, ascidian larvae do not normally disperse very far, often just a few metres or less especially in colonial species (for review see Ayre et al. 1997).

Broadcast spawning solitary species would be expected to have a greater dispersal of gametes and larvae than brooding species both colonial and solitary, and this prediction holds true for some species like those investigated by Ayre et al. (1997), who measured allozyme variation between populations of a solitary broadcast spawner, a brooding social, and a brooding colonial species to determine actual dispersal. In the solitary broadcast spawners *Ciona intestinalis* (L., 1767) and *Asciidiella aspersa* (Müller, 1776), sperm conserve energy, and thus longevity, by delaying maximum activity until chemically activated by and attracted to homo-specific eggs (Bolton and Havenhand 1996; Yoshida et al. 2003). However, these species typically occur in large masses, and mass spawning results in clouds of gametes that quickly fertilize, with dispersal actually being quite limited. The colonial species *Diplosoma listerianum* (Milne-Edwards, 1841) (Bishop 1998) and *Botryllus schlosseri* (Pallas, 1766) (Johnson and Yund 2004) have surprising sperm longevity; sperm are apparently quiescent until taken in by feeding zooids and activated only when close to ovulated eggs; nevertheless numerous studies have shown highly limited dispersal in both species. Molecular genetics is proving to be an indispensable tool for determining dispersal distances (Ayre et al. 1997; Sommerfeldt and Bishop 1999), the presence of cryptic species (Turon et al. 2003), and possible origins of nonindigenous species (Geller 1996; Castilla et al. 2002; Stoner et al. 2002; Turon et al. 2003). Thus, hypotheses of dispersal potential based on maximum gamete and larval life need to be investigated for the individual species. Such factors as limiting water circulation patterns, brooding, release of ga-

metes in a sticky mucous string, and larval behavior including gregarious settlement often result in limited dispersal in most solitary as well as colonial species (Lambert 1968; Bingham and Young 1991; Havenhand 1991; Lambert et al. 1995; Petersen and Svane 1995; Carballo 2000). A few species, primarily molgulids, are direct developers with sticky eggs that develop into anural larvae; dispersal is especially limited (Young et al. 1988; reviewed by Bates 2002, 2005). In the encrusting colonial species *Protostyela longicauda* Monniot, Vázquez, and White, 1995, the brooded larvae are released and then metamorphose before hatching one or more hours after release in laboratory experiments (though possibly sooner in nature). They do not swim but have an unusually long coiled sticky tail (composed of tunic only and thus nonmuscular) that attaches to seaweeds in a high-energy rocky coastal area of northwestern Spain (Turon and Vázquez 1996).

The tadpoles of most species become negatively phototactic at the time of settlement (see review in this issue by McHenry 2005), and thus, choose shaded locations especially on the sides or undersides of solid structures, an adaptation undoubtedly beneficial in decreasing radiation, sedimentation, and algal overgrowth (see review by Svane and Young 1989; Hurlbut 1993). In a few species, however, the tadpoles are photopositive when ready to settle (e.g., *Polyandrocarpa zorritensis* (Van Name, 1931); Vázquez and Young 1998). This might also be the case for species with photosynthetic symbionts. Stoner (1994) followed individual larvae of *Diplosoma similis* (Sluiter, 1909) by SCUBA from release to settlement; the colonies were situated in shallow coral reef areas exposed to light and were easily observable. The motile colonies of *Didemnum molle* (Herdman, 1886) with their *Prochloron* symbionts move to areas of favorable light intensity for photosynthesis after larval settlement in shaded locations because the larvae and juveniles cannot survive in full sunlight (Olson 1983).

Anthropogenic transport has caused the successful invasion of most harbors of the world by nonindigenous ascidians as well as other taxa. The most likely vectors of transport of ascidians are probably hull fouling beginning several hundred years ago (Monniot et al. 1991; Monniot and Monniot 1994; Carlton and Geller 1993; Hewitt et al. 2004) and perhaps to a lesser extent via introduced oysters, mussels, seaweeds, and other biota carrying settled individuals or colonies on their surfaces. Once the long-distance transport of a species has resulted in successful colonization of a new harbor, the species almost always seems to spread quickly to neighboring harbors probably on hull-fouled small craft (Wasson et al. 2001; Lambert and Lambert 1998, 2003; Brunetti and Mastrototaro 2004).

There is a crucial need for more knowledge about ascidian ecology and physiology because some species that are extremely tolerant of a wide range of environmental conditions have become significant economic problems by fouling docks, ship hulls, and farmed oysters and mussels (for reviews see Monniot and Monniot 1994; G. Lambert 2001, 2002; Carver et al. 2003; Lambert and Lambert 2003). At many sites, ascidians are competitively superior dominant foulers on these artificial surfaces, which are unstable environments with lower biodiversity and thus lower resistance to invasion than healthy natural ecosystems (Stachowicz et

al. 2002a.). Artificial structures are often the first surfaces colonized by newly arrived nonindigenous species, a few of which after successfully becoming established have expanded their populations to natural environments with deleterious effects on native species. There may be fewer than a dozen species present at any one site, but their rapid growth and attainment of sexual maturity in just a few weeks, their tolerance for high levels of pollution, siltation, and environmental fluctuations such as temperature and salinity plus a lack of predators results in the establishment of huge populations. In fact, the most common fouling species seem to thrive on the high nutritive value of suspended matter in harbors. Some of the most successful invading species with a worldwide distribution are listed by G. Lambert (2001).

Although usually confined to harbors, in some cases these invaders can colonize natural subtidal areas and quickly overgrow and smother the native fauna, thereby significantly changing the benthic community. The large *P. praeputialis*, an invader to Chile from Australia (Castilla et al. 2002), is now so abundant on rocky shores of Antofagasta Bay that it has completely modified the habitat, creating shelter for 116 species compared with 66 species on adjacent rocky shores lacking *P. praeputialis*; Castilla et al. (2004) have dubbed this “ecosystem engineering”. Another recent example of an invader causing dramatic changes to the benthos is *Didemnum* sp., which has invaded both coasts of the U.S. and apparently also New Zealand (molecular genetics analysis is underway to confirm this) and is rapidly expanding its territory and biomass in all these areas as well as France, the Netherlands, and possibly also Japan. In addition to inshore sites in New England, it now covers 50%–90% of a recently surveyed 70-km<sup>2</sup> area of the seabed on the Georges Bank, 265 km from the coast and at a depth of about 46 m, and appears to be smothering scallops and other sessile marine life (P. Valentine, personal communication); additional shelf areas may be affected that have not yet been surveyed by remote cameras. Its mode of transport is not known, but it fragments easily and may have arrived in ballast water and then spread to secondary sites by fishing boats and their gear, or may have been introduced with imported oysters. Like many other colonial species (Stoner 1989; Stocker 1991), *Didemnum* sp. fragments can quickly attach to solid substrates and grow asexually into large colonies (L. Harris, personal communication). There are no publications yet on the spread and impact of this species, but information is available on the US Geological Survey Woods Hole Science Center Web site (Valentine 2004).

*Perophora japonica* Oka, 1927, a native of Japan (Nishikawa 1991), colonized the coast of France on the English Channel in the 1980s (Monniot and Monniot 1985) and more recently the south coast of England (Nishikawa et al. 2000; Baldock and Bishop 2001). It was recorded from northern California for the first time in 2003 (Lambert 2005). The Japanese species *Botrylloides violaceus* Oka, 1927 continues to spread around the northern hemisphere in temperate waters (for review see Lambert and Lambert 2003). The worldwide spread of another native of Japan *Styela clava* Herdman, 1881 during the 20th century, including its appearance in Australia, has been well documented (for review see Lambert and Lambert 1998). Other trans-hemisphere introductions include the European species *A. aspersa* re-

corded in New Zealand by Brewin (1946) and *C. intestinalis* in Australia (Van Name 1945), *Styela plicata* (Lesueur, 1823) (country of origin not known but thought to be the northern hemisphere) and the northeast US *Molgula manhattensis* (DeKay, 1843) in Australia (Kott 1985). *Polyandrocarpa zorritensis*, described from a sandy substrate in northern Peru (Van Name 1931), appeared in northern Italy in the 1970s (Brunetti 1978–1979) and in southern California in the 1990s (Lambert and Lambert 1998). The southern hemisphere *Corella eumyota* Traustedt, 1882 recently appeared in two harbors in Brittany, France (Lambert 2004), and is likely to spread farther in the northern hemisphere.

Naranjo et al. (1998) compiled distribution data for 519 Atlantic and Mediterranean ascidian species; they found very few common to both sides of the Atlantic other than those known to be associated with anthropogenic transport. Half the species have very limited distribution, and correlated with that, the highest diversity was found for the Caribbean and Mediterranean. Various transition zones, primarily latitudinal, are indicated. Based on an exhaustive analysis of a very large data set, the authors propose “a new distribution of general zoogeographical areas...in correspondence with the principal marine areas of endemism found for shallow-water ascidians”. This important synthesis of the biogeography of Atlantic and Mediterranean species provides a significant baseline for charting and understanding future distributional changes.

#### **Food and reproductive seasonality**

Like the planktonic Tunicata (see below), nearly all ascidians are ciliary–mucus filter feeders that utilize very small particulate matter primarily in the 0.5–2 µm range (Flood and Fiala-Medioni 1981; Coma et al. 2001; Tatián et al. 2002; Bone et al. 2003), although they do take larger particles including their own gametes (Young 1988; G. Lambert, unpublished observation). When present in large numbers, their high filtration rate can have a dramatic effect on available plankton and suspended organic matter (Hily 1991; Coma et al. 2000; reviewed by Riisgård and Larsen 2000). Petersen and Riisgård (1992) estimated that the huge late summer populations of *C. intestinalis* are capable of filtering a volume of water equal to the entire volume of a shallow Danish fjord every day. Reproductive season usually coincides with the period of maximum food production (i.e., when phytoplankton productivity is highest). This is summer in temperate regions but autumn in the Mediterranean; peak summer temperatures cause stratification of water layers and a depletion of food supply for benthic suspension feeders, many of which go dormant. However, as the water cools in autumn the thermocline breaks down and mixing brings nutrients from deep water (Becerro and Turon 1992; reviewed in Coma et al. 2000). There are numerous species with continuous breeding throughout the year in both temperate and tropical regions, although even in these species there is usually a late-summer peak (Goodbody 1961; Lambert 1968; Lambert and Lambert 2003). In the Antarctic species where seasonal temperature differences are minimal, gametes of *Cnemidocarpa verrucosa* (Lesson, 1830) mature and are released during the winter (Sahade et al. 2004). It is possible that the animals put all their energy into accumulating food reserves during the summer when phytoplankton blooms oc-

cur and then use these reserves for reproduction during the winter. On the other hand, the diet of this species includes suspended organic matter that because of seasonal differences in mixing and resuspension of benthic sediments may actually result in a higher food supply during the winter (Tatián et al. 2002). When warm temperature and abundant food is available, *B. schlosseri* colonies maximize female reproduction (number of eggs produced), while at lower temperatures and food supply male reproduction is emphasized (Newlon et al. 2003).

Ascidians' efficient filtration abilities may be the key to recent population explosions of various species in regions close to expanding human populations and coastal development, and may be tied to increasing bacterial densities and suspended sediments (Bak et al. 1996, 1998). The large amount of fecal matter produced is an important contribution to microbial food webs and detritus for deposit feeders (Guidi and De Morais 1983). As fecal pellets age and acquire a microbial community, hydrodynamics can resuspend this material along with other microbial-rich detritus, thus recycling it for ascidians and other suspension feeders (Tatián et al. 2002). Colonial ascidians harboring symbiotic algae, particularly *Prochloron*, are known to derive significant nutritional benefit from this association (see below under Symbionts). A few abyssal phlebobranchs and the abyssal Sorberacea have lost their filter-feeding capability and have become modified for a carnivorous life style, feeding on small crustaceans and polychaetes (Monniot and Monniot 1990, 1991; see below under Abyssal species).

### Competition

Competition, both intra- and inter-specific, for space and food affects the life-history strategies of many ascidians, including the earliest stages. Interspecific competition by sperm to fertilize eggs may be an important factor in determining ultimate success of the species (Lambert 2000; G. Lambert 2001). There appears to be a trade-off in strategies for occupying space: some species remove their neighbors by overgrowth or inhibition of settlement, while others limit available space by creating dense mono-specific aggregations. The sponge *Haliclona* Grant, 1836 produces an alkaloid that induces *Herdmania momus* (Savigny, 1816) tadpoles to settle but then inhibits completion of metamorphosis, thus resulting in death of the tadpole (Green et al. 2002). Tunic or extracts from aggregating species have been shown to induce settlement and metamorphosis of larvae of that species, while not affecting larvae of other species (reviewed by Svane and Young 1989); benefits include decrease in predation and in one case protection from dessication. On the other hand, presence of a colony of *Clavelina moluccensis* (Sluiter, 1904), a social species that produces large clonal clumps of individuals, is apparently inhibitory to larval settlement, thus resulting in a nonrandom spacing of the colonies (Davis and Campbell 1996). The botryllids employ an active method of preventing overgrowth by using their well-developed allorecognition system; interactions of the vascular ampullae of unrelated colonies usually leads to "a hemolytic rejection reaction" (reviewed by Hirose 2003) either upon contact or after initial fusion to form a chimera (Chadwick-Furman and Weissman 2003), while very closely

related colonies or pieces of the same colony will successfully fuse. Fusion of genetically identical or nearly identical colonies also occurs in a number of aplousobranchs. Fusion and fission have been followed in several didemnids; fission results in faster growth of the smaller genets, which may subsequently fuse upon contact (Ryland et al. 1984; Stoner 1989; Stocker 1991). Bak et al. (1981) estimated that because of this life-history trait clones "may survive indefinitely".

The alternation of generations by salps and doliolids between sexual and asexual phases allows a quick response to favorable conditions such as phytoplankton blooms, resulting in rapid increase in number. This "ability to invade and rapidly occupy an ecological niche" by asexual reproduction is termed "ecological efficiency" (R. Christen and J.-C. Brannonot in Bone 1998). The same phenomenon occurs in many colonial ascidians, as they rapidly occupy space on benthic substrates and overgrow more slow-growing competitors (G. Lambert, unpublished observation). A similar rapid response to favorable environmental conditions occurs through sexual reproduction in self-fertilizing solitary ascidians such as *C. inflata* and *C. eumyota* (Lambert 1968, 2004). A special case of rapid space utilization occurs in *D. listerianum* where nonidentical clones commonly fuse to form chimeric colonies composed of multiple genotypes that theoretically could interbreed (Sommerfeldt and Bishop 1999). This adaptive strategy has no doubt been an important factor in this species' worldwide distribution, which is the result of numerous introductions. Other competitive strategies are discussed below in the antifouling section.

Rapid growth and precocious attainment of sexual maturity are characteristic of most fouling species. Especially in harbors, when artificial (man-made) or shallow natural surfaces are denuded by storms, heavy rainfall, temperature extremes, or other factors, they are often quickly colonized by both solitary and colonial ascidians, with very high biomass production in only a few weeks. Successful solitary species such as *C. intestinalis*, *C. savignyi*, and *S. clava* do well on harbor structures under crowded conditions; they may reach 15 cm in length, which allows them to extend out into the water farther than most non-ascidian taxa (Lambert and Lambert 1998, 2003). On the other hand, in natural environments with high species diversity and stable environmental conditions, the available space is fully utilized and new settlers (including invading species) are much less likely to become successfully established (Paulay et al. 2002; Stachowicz et al. 2002a).

### Predation

A wide variety of predators feed on ascidians (for review of earlier papers see Millar 1971). Newly settled juveniles are eaten by various polychaetes, gastropods, crabs (Davis 1988; Ivanov 1993), and other motile carnivorous or omnivorous invertebrates (Turner and Todd 1991), and fish (Hurlbut 1991). Predation at this vulnerable stage can be highly significant in shaping the adult community that develops and persists (reviewed by Osman and Whitlatch 1996, 1998). A number of flatworms eat adult as well as juvenile ascidians: *Eurylepta leoparda* Freeman, 1933 enters the oral siphon of *C. inflata* and eats the entire body but leaves the

tunic untouched (Lambert 1968; Ching 1977); *Stylostomum sanjuaniana* Holleman, 1972 drills into the tunic of several colonial species and sucks out the zooids while ingesting a minimum of tunic; *Pseudoceros canadensis* Hyman, 1953 feeds similarly on *Distaplia occidentalis* Bancroft, 1899 (G. Lambert, unpublished observation), as does the tropical *Pseudoceros indicus* on two *Eudistoma* spp. (Newman and Schupp 2002) and *Maritigrella crozieri* (Hyman, 1939) on the Caribbean social species *Ecteinascidia turbinata* Herdman, 1880 (Newman et al. 2000). The prosobranchs *Lamellaria* spp. are apparently species-specific to their prey and are cryptically colored to match the prey: zooids of *Cystodytes lobatus* (Ritter, 1900) are eaten by *Lamellaria diegoensis* Dall, 1885 (Lambert 1980); *Lamellaria stearnsii* (Dall, 1871) is found only on *Trididemnum opacum* (Ritter, 1907) (for review see Morris et al. 1980). The carnivorous gastropod *Concholepas concholepas* (Bruguere, 1789) is a significant predator of *Pyura chilensis* Molina, 1782 (Stotz et al. 2003). A review of molluscan predators from 14 prosobranch families that feed on adult ascidians is given by Dalby (1989), which does not include a number of nudibranchs (reviewed by Thompson 1964). Rock crabs *Cancer irroratus* Say, 1817 ate up to 11 adult *C. intestinalis* per day in laboratory trials (Carver et al. 2003). Numerous species of sea stars are major predators of various solitary ascidians (Paine and Suchanek 1983; Svane 1983; O'Clair and O'Clair 1998). A number of fish species eat colonial and solitary ascidians (Stoner 1990; Raveendran and Harada 1996; Osman and Whitlatch 1996, 1998). Birds may also eat significant numbers of adult ascidians: 40 of 48 oystercatchers *Haematopus palliatus pitanay* (Murphy, 1925) were observed feeding on attached adult *P. praeputialis* at low tide and wave-dislodged individuals at high tide at a rocky intertidal seashore at Antofagasta, Chile, by stabbing holes through the tunic of these very large ascidians and removing the bodies (Pacheco and Castilla 2001). An interesting aspect of this feeding behavior is that *P. praeputialis* is nonindigenous in Chile (Castilla et al. 2002) and is restricted in distribution to this single area where it is very abundant. Sea otters eat *P. chilensis* (Rozzi and Torres-Mura 1990). In Australia humans use large numbers of *P. praeputialis* as fish bait (Kingsford et al. 1991), a practice that disturbs the tight clumps and the composition of invertebrate populations within these patches (Monteiro et al. 2002).

Ascidians are a human food source in many parts of the world (Monniot et al. 1991). Only a few species are economically important and all are stolidobranchs. *Halocynthia roretzi* (von Drasche, 1884) and *Halocynthia aurantium* (Pallas, 1787) are farmed in Japan; *H. roretzi* and *S. clava* are farmed in Korea. Both countries export these species to Europe and North America. *Microcosmus sabatieri* Roule, 1885 and *Microcosmus vulgaris* Heller, 1877 are eaten in Europe (referred to in fish markets as the sea violet), while *P. chilensis* is an important food item in Chile (Davis 1995). The Maoris of New Zealand were known to eat a native *Pyura*.

For reasons that are as yet not fully understood, floating artificial structures in harbors provide a unique environment that results in the establishment of invertebrate assemblages not duplicated on natural benthic surfaces (Connell 2000; Holloway and Connell 2002; Paulay et al. 2002; Lambert

and Lambert 1998, 2003). One important factor is that they are subject to less predation by benthic predators. The presence of these artificial habitats can lead to an overall increase in species diversity within harbors (Connell and Glasby 1999).

#### ***Antipredator and antifouling defenses: mechanical, physical, and chemical***

Post-settlement survival of some species is greatly enhanced by settlement in locations protected from predation, such as under algae (Stocker and Bergquist 1987) or in rock crevices (Svane and Young 1989). Predation usually decreases dramatically once the recruits have passed the vulnerable first week or so (Osman and Whitlatch 1998); competition then probably becomes the most important determinant of survival to reproductive maturity.

Periodic sloughing or exfoliation of the surface layer of the tunic occurs in a number of ascidians, either naturally as in *Pyura pachydermatina* (Herdman, 1881) (Lambert and Lambert 1997) and *Polysyncraton lacazei* (Giard, 1872) (Wahl and Banaigs 1991) or as a result of gentle abrasion as in *P. nigra* (G. Lambert, personal observation) and *C. lobatus* (Lambert 1979), which also produces copious mucus in response to rubbing. Tiny sharp calcium carbonate spicules project from the tunic of *Herdmania* spp. (Lambert and Lambert 1987; Lambert 1992); molluscan grazers avoid crawling over the tunic surface and spines broken off during handling caused irritation and inflammation of my skin. A similar defense is evident in the spicule-covered tunic of *Bathypora feminalba* Young and Vázquez, 1995, which lives on high-current rock walls and crevices along the northeast Pacific coast of British Columbia where it would no doubt be subject to high predation pressure (Young and Vázquez 1995; Lambert 1998).

Many ascidians, like sponges and bryozoans, avoid predation or fouling by producing noxious secondary metabolites (Lindquist et al. 1992; Teo and Ryland 1994, 1995; Davis 1998; Vervoort et al. 1998; Pisut and Pawlik 2002; Joullie et al. 2003; McClintock et al. 2004). Perhaps it takes a juvenile several days or weeks to produce and store its full complement of metabolites; Osman and Whitlatch (1996) found that avoidance is sometimes incomplete until at least a week or two after settlement, which would explain many predators' preference for young stages. In certain species the metabolites are transferred unchanged from adults to the eggs and larvae (reviewed by Teo and Ryland 1994), or even to the predators, which in turn acquire the same chemical defense (Paul et al. 1990; Newman and Schupp 2002). A number of these biochemicals, although present in tiny amounts, have been isolated and shown to have cytotoxic effects of great promise in the pharmaceutical industry. *Ecteinascidia turbinata* is under cultivation for its metabolite ecteinascidin in phase II trials (Carballo et al. 2000; Mendola 2003). The active compounds may be restricted to certain tissues (Pisut and Pawlik 2002) or in some cases are actually produced by algal, fungal, or bacterial symbionts that are present in many colonial ascidians, especially tropical species. Wahl (1995) found a negative correlation between epibiosis and the presence of photosynthetic microbial symbionts in several species of didemnids. There is now a large body of literature on

natural products isolated from many species of ascidians and their possible pharmacological applications (for reviews see Faulkner 2000, 2002; Rinehart 2000). In some cases, predation or palatability is related more to potential food value of the adult or larval prey item than to toxic natural products (Tarjuelo et al. 2002).

Many species especially phlebobranchs take up vanadium into the blood to a concentration several thousand or more percentage higher than that of seawater. Its functions are not thoroughly understood, but a high level of vanadium in the tunic is toxic to larvae and prevents epibiosis, and high vanadium levels in body tissues make them unpalatable to potential predators such as fish (Stoecker 1980). Another antipredator, antifouling defense of many colonial and solitary species is very low pH of the tunic owing to sulfuric and (or) hydrochloric acid in bladder cells that rupture easily (Lambert 1979; Pisut and Pawlik 2002). Several mechanisms, providing a redundancy of defensive strategies, may operate in the same species (Wahl and Banaigs 1991; Pisut and Pawlik 2002). Nearly all colonial species maintain a clean, unfouled surface, a clear indication of the presence of at least one antifouling strategy. A number of solitary species, particularly stolidobranchs with thick leathery tunics or surface hairs or tubercles, become heavily fouled and cryptic; this may be a different antipredator strategy, since the body tissues of these species when removed from the tunic are highly palatable to fish and other predators including humans.

#### **Symbionts, parasites, and commensals**

The nutritional benefits of unicellular algal and prokaryote symbionts to the host are well documented (Kott 1982; Lewin and Cheng 1989; Trench 1993; Koike and Suzuki 1996). Most species with photosynthetic symbionts are tropical colonials in the family Didemnidae and in many cases the relationship is an obligatory mutualistic symbiosis. The larvae have special structures to gather and carry the algal cells prior to liberation from the parent colony (Hirose 2000). The host may display adaptive behaviors to maximize the photosynthetic output of the symbionts (Olson 1983; Ryland 1990). Other unicellular endobionts are suctorians and other ciliates (O'Clair and O'Clair 1998); species of parasitic apicomplexan gregarines unique to ascidians (Scippa et al. 2000; Ciancio et al. 2001) and a haplosporidian (Ciancio et al. 1999). The molgulid renal sac harbors the endosymbiont protist *Nephromyces* Giard, 1888, within which are intracellular bacteria; these organisms are associated with nitrogen metabolism (Saffo 1990).

Besides unicellular symbionts, many ascidians harbor one or more multicellular endobionts; both groups were extensively reviewed by Monniot (1990), with descriptions and morphology of numerous interactions. The most familiar endobionts are parasitic copepods (Ooishi and Illg 1977; Illg and Dudley 1980; Gotto 1993; Dalby 1996), which are usually specialized to live in one or more of the host's internal organs. Amphipods live in the branchial sac of most solitary species (Dalby 1996; Thiel 1999, 2000) and feed on the mucous sheet produced by the host. The amphipod *Polycheria osborni* Calman, 1898 makes a shallow burrow in the surface tunic of various colonial ascidians and orients itself ventral side up; it creates a feeding current by rhythmic beat-

ing of the pleopods (Skogsberg and Vansell 1928; Lambert 1979). The bivalve *Mytilimeria nuttalli* Conrad, 1837 is also found embedded in a variety of colonial ascidian species, apparently its exclusive habitat (Yonge 1952; Lambert 1979). Other symbionts recorded from ascidians include nemerteans (for review see Dalby 1996), pinnotherid crabs (Kozloff 1987), the cnidarian *Bythotiara huntsmani* (Fraser, 1911) in the oral siphon of *Ascidia paratropa* (Huntsman, 1912) and *Ascidia columbiana* (Huntsman, 1912) (Mills and Miller 1987; O'Clair and O'Clair 1998), and microfilamentous algae in the tunic matrix of several New Zealand species (Lambert et al. 1996). The exact relationship between host and symbiont for many of these species has not been determined.

#### **Resource allocation**

The amount of energy invested in structure versus reproduction varies widely between species, with colonials in general investing a larger percentage of available energy to reproduction than solitary species (Tarjuelo and Turon 2004). Resource allocation also varies by temperature and food availability within each species (Carver et al. 2003; Newlon et al. 2003). Several long-term life-history studies published since Millar's (1971) review encompass a wide range of findings and thus do not fit tidily into one or another of the above categories. Svane (1983), in summarizing 12 years of observations on four co-occurring solitary ascidians in Sweden, showed that each of these abundant and successful species uses different ecological strategies, with variations in such factors as reproductive season, size, shape, longevity (from a few months for *C. intestinalis* to more than 12 years for *Pyura tessellata* (Forbes, 1848)), predation, and overgrowth vulnerability. Turon and Becerro (1992) documented the life histories of several co-occurring colonial species in the Mediterranean and also found a variety of successful strategies. A species' success, or fitness, is measured by its ability to survive to reproductive maturity and leave sufficient offspring to not only perpetuate itself but also to increase if possible. The many hundreds of ecological papers on ascidians that have been published since Millar's (1971) review are a testament to the diversity of the successful life-history strategies that exist.

#### **Abyssal species**

The deep-sea environment is home to many tunicate species, most of them very different in morphology from their shallow water relatives. Only a few species have been recorded that live at both shallow and abyssal ( $\geq 2000$  m) depths. Most abyssal ascidians are solitary stolidobranchs; there are not many phlebobranch species and the aplousobranchs are for the most part absent. In addition to the ascidians, there are a number of species of tunicates so highly specialized and different in morphology that Monniot et al. (1975) placed them in their own class Sorberacea. There is disagreement as to whether the Sorberacea are sufficiently different to warrant being in their own class or have evolved from molgulid ascidians (Kott 1989, 1998); as yet no molecular comparisons have been made. I will sidestep this taxonomic controversy and concentrate on the remarkable morphological adaptations of abyssal forms to this particular environment.

Extensive reviews of the distribution and ecology of abyssal tunicates have been published by Monniot and Monniot (1975a, 1975b, 1978, 1990). They emphasize that adaptations are based primarily on the composition of the substrate and available food. Although most shallow-water species are found only on hard substrates (with the exception of some molgulids adapted to soft sediments), the abyssal plains of the world's oceans are mostly soft mud, but nevertheless harbor numerous species belonging to various families. Tunicate species diversity is highest in shallow waters: there is a large decrease to a minimum between 1500 and 2000 m (bathyal), then a surprising increase with increasing depth to a peak at 4000–4500 m — 124 known species below 2000 m as of 1975. Many abyssal species have a very wide distribution that includes several oceans, probably a consequence of the stable environment which exists over thousands of square kilometres of sea floor. Nothing is known of their life expectancy, but they are most likely slow growing. Abyssal tunicates are surprisingly abundant, with sometimes hundreds of individuals and up to 20 species collected in a single dredge haul (Monniot and Monniot 1978).

The most dramatic difference between shallow and abyssal tunicates is reduction in size. Food is scarce; while littoral species are suspension feeders, there are no phytoplankton at abyssal depths and a much lower concentration of suspended matter. The scarcity of aplousobranchs is thought to be a result of there not being enough food to support small zooids with a low proportion of branchial sac relative to body and tunic than in solitary species (Monniot and Monniot 1975a, 1978). Several types of morphological changes have evolved in abyssal species, all involving the branchial sac which is thin, delicate, and greatly reduced in complexity; however, in many species, it is increased in size relative to body size (exceptions are the Octacnemidae and Sorberacea; see below). Even though these species are living on soft mud, the branchial sac does not get clogged with sediment, which indicates that bottom currents are very low. A number of abyssal species resemble shallow-water phlebobranch or stolidobranch relatives but are tiny and spherical, ranging from 0.5 mm to a few millimetres in length. Ciliated stigmata are reduced but present, and food is trapped on a mucous sheet as in littoral species. In a second type of convergent evolution among abyssal aplousobranchs, phlebobranchs, and stolidobranchs, the branchial sac consists of a flat delicate mesh of unciliated openings separated by transverse and longitudinal vessels. Most, such as species of *Culeolus* Herdman, 1881, are stalked; the slender stalk may be as long as a metre. The widely separated siphons gape, a mucous sheet lining the branchial sac traps particles; therefore, it is possible that the animals orient passively in the current in a way that allows the water to flow through the sac passively, similar to the littoral species *P. pachydermatina* (Lambert and Lambert 1997).

A third group of species has evolved from suspension feeding to carnivory. In the phlebobranch family Octacnemidae, the oral siphon is hypertrophied to form two large lips (*Dicopia* Sluiter, 1905, *Megalodicopia* Oka, 1918, and *Situla* Vinogradova, 1969) or eight lobes (*Octacnemus* Moseley, 1876), which capture small crustaceans and other motile prey. The branchial sac is much reduced and the stigmata are unciliated, but macroscopic prey as well as fine

suspended matter are trapped on a mucous film that is formed into a cord and passes through the digestive tract. Octacnemids are unusually large for abyssal species, some reaching 10 cm or more in length. They apparently keep the oral opening widely gaping, using energy to close it only when prey is caught (Okuyama et al. 2002). The most specialized abyssal species belong to the class Sorberacea (following Monniot and Monniot 1990) or the family Hexacrobylidae of the Stolidobranchia (following Kott 1989, 1998). All are carnivorous on motile prey, including small crustaceans, nematodes, and polychaetes. The oral siphon is lobed and muscular, the branchial sac with a few very small openings is reduced to a ring around the base of the oral siphon, while the gut is greatly expanded with diverticula that may be lobed. This is the only group that lacks a true endostyle. Prey become coated with mucus produced by cells lining the digestive tract (Gaill 1979).

All abyssal soft-bottom species both stalked and unstalked have numerous posterior rhizoidal extensions of the tunic that anchor them in the soft substrate and hold the siphons above the sediment. The tunic of many species is covered by foraminifera. The reasons for this are unknown, but they may just be providing a solid substrate for the foraminifera, which in turn give a rigidity to the soft transparent tunic. All species are hermaphroditic, and reproduction is apparently always oviparous. No brooded larvae have been found.

#### **Classes Appendicularia and Thaliacea — all planktonic**

An excellent, comprehensive review of all aspects of the biology of these two classes was recently published by Bone (1998). A brief summary of their ecology and natural history will thus suffice; all information is from Bone (1998) unless otherwise indicated.

Appendicularians are among the most common zooplankton and occur in all oceans. Like the ascidians, they feed by means of a mucous pharyngeal filter that traps particles a few micrometres or less in size (Bone et al. 2003). The Appendicularia (also called larvaceans) are solitary and are only a few millimetres in length; they form a gelatinous "house" (5–7 cm in the largest species) that by means of a complex water circulation pattern can concentrate sub-micrometre-sized colloidal and macromolecular particles into aggregates before trapping them on the filter for ingestion. This feeding strategy allows them to utilize a size range of particles not available to other planktonic filter feeders, producing a transfer of energy from the microbial level directly to higher trophic levels and by-passing the so-called microbial loop. They are major consumers of small phytoplankton and other particles in the range of 2–8  $\mu\text{m}$  (Fernández et al. 2004), although much larger phytoplankton may comprise the diet of some species during blooms. Small individuals efficiently retain smaller particles than do larger individuals of the same species (Fernández et al. 2004); thus, there are changes in diet with age. Most appendicularians occur at depths above 200 m, but there are permanent populations at aphotic meso- and bathy-pelagic depths, indicating a stable source of nutrients because this group has no adaptations for storing food energy. When a house can no longer be unclogged, it is discarded; an individual may make up to 5 houses per day. Life span is one to a few days, but blooms may persist for weeks; numbers greater than 25 000 per cu-

bic metre have been recorded, resulting in a major part of the water mass being filtered per day. Fecal pellets and discarded houses form a significant percentage of marine "snow" as they descend, providing an important food source for other organisms. Houses can vary in nutritional content by season and by species; discarded houses sink faster but also decay faster at higher temperatures. In the Mediterranean around Villefranche-sur-Mer, where appendicularians have been well studied, there is a repeatable seasonal species succession pattern apparently dependent on primary production and temperature. Occasionally swarms of appendicularians without houses are encountered, which are thought to be breeding aggregations.

Copepods, fish larvae and small fish, medusae, foraminifera, and chaetognaths consume living appendicularians and their houses, as well as discarded decaying houses with their additional microbial complement. Defensive strategies include bioluminescence of the houses in response to external stimuli; different species display different patterns. The non-luminescent *Oikopleura longicauda* (Vogt, 1854) avoids predators by tumbling away with its house when prodded. Many species abandon their houses when disturbed; the individual is very much smaller than the inflated house, can swim away quickly, and then form a new house.

Thaliaceans (salps, doliolids, and pyrosomes) are also a major component of the plankton in all oceans except the Arctic. Though most species have a wide distribution, there are species differences between nearshore and open-ocean regions. Pyrosomes are found only in warmer waters. Thaliaceans are colonial, although salps and doliolids have complex life cycles that include a solitary stage. Sizes vary immensely; doliolids are the smallest at about 2 cm or less, some salp species may reach 20–30 cm in length, while pyrosome colonies of the largest species are up to 20 m in length (Kozloff 1990). Dense swarms several thousand per cubic metre extending several to many square kilometres are common, may persist for weeks, and have a significant impact on other components of the plankton. In the Antarctic, for example, salps may eat a majority of the eggs and larvae of krill. Unlike appendicularians, many salps and pyrosomes migrate vertically in a daily range up to 1000 m or more. Special luminescent bacteria are present in most pyrosomes; luminescence is under the control of the host, but its function is not known, although the patterns are species-specific and light emission levels can be quite high. Most doliolids remain in the upper photic zone, although with advances in collecting techniques a few mesopelagic species have recently been discovered (Godeaux and Harbison 2003). Particles under 1 µm can be captured on the mucous pharyngeal filter, but retention is much higher for particles larger than 2 µm (Bone et al. 2003). Particle size preference seems to be related at least in part to adult zooid size. Phytoplankton is the primary food source. Because of the diel migration of many species, most feeding takes place near the surface, while fecal pellet production may predominate at depths to several hundred metres, thus hastening the downward flux of pellets to mesopelagic and abyssal depths. Thaliaceans and their byproducts are an important food source for many pelagic carnivores, including radiolarians, medusae, ctenophores, heteropods, octopods, copepods, amphipods, fish, and even sea urchins, sea turtles, and birds. Over 70 species of fish

are known to eat thaliaceans as a significant part of their diet. Some predators are parasitic as juveniles, such as the medusa *Aequorea* Peron and Lesueur, 1809. The octopod *Argonauta* L., 1758 uses salps for both food and shelter.

Since Bone's (1998) review, a number of ecological papers on this important group have appeared that advance our understanding of the functional morphology of pelagic tunicates, especially of the gut and feeding apparatus (Bone et al. 2003), and their role and importance as consumers and secondary producers (Capitanio et al. 1997; Bochdansky and Deibel 1999; Greenwood et al. 2001; Gibson and Paffenhöfer 2000, 2002; Vargas et al. 2002; Flood 2003; López-Urrutia et al. 2003a, 2003b; Sato et al. 2003; Touratier et al. 2003; Fernández et al. 2004). Ecological factors have no doubt provided a driving force for evolutionary changes, many of which remain obscure as efforts intensify to elucidate the phylogenetic relationships within the Tunicata.

### Subphylum Cephalochordata

There is a large body of literature on this small group of about 30 species comprising one family with two genera (Poss and Boschung 1996; Nishikawa and Nishida 1997). Most research has been on their morphology, embryology, organ function, molecular sequencing, and gene expression because of their pivotal phylogenetic position. Commonly called amphioxus or lancelets, they bury vertically in the surface layer of sand and filter-feed by means of a branchial ciliary current that passes water through a mucous sheet as in the other protochordates. *Branchiostoma floridae* Hubbs, 1922 are capable of trapping particles from the microbial to small phytoplankton size (Ruppert et al. 2000); *Branchiostoma lanceolatum* (Pallas, 1774) traps particles primarily  $\geq 4 \mu\text{m}$  on its mucous filter (Riisgård and Svane 1999). Some species were found with surface detritus in their gut (Nishikawa et al. 1997), but this was probably ingested during feeding. Riisgård and Svane (1999) observed that while filter-feeding *B. lanceolatum* "coughs" periodically by closing the excurrent opening and contracting the body to dislodge excess detritus clogging its filter and force it back out of the mouth. The commonest habitats are shallow subtidal tropical, subtropical, and temperate sand flats. They prefer coarse sand with fairly fast water flow and do not inhabit silty sediments (Berrill 1987; Nishikawa et al. 1997). When disturbed they quickly leave their burrow and swim fast a short distance, then rapidly burrow again posterior end first into the sand. Population densities up to several thousands per square metre have been recorded for *B. floridae* (Ruppert and Barnes 1994; Stokes 1996; Ruppert et al. 2000); 1.1 million metric tons of planktotrophic larvae were estimated to be produced by *Branchiostoma senegalense* Webb, 1955 in northwest Africa (Flood et al. 1976). Life span is surprisingly long, 2–5 years depending on the species, with a spring and summer breeding season (Stokes 1996; Whittaker 1997). Sexes are separate, spawning occurs at or after sunset, and fertilization is external (Tung et al. 1958; Ruppert and Barnes 1994; Stokes and Holland 1996; Holland and Wada 1999). Planktonic larval life lasts about 4 weeks, depending on temperature (Stokes and Holland 1995). The predominant larval behavior is hovering, which is controlled by coordinated beating of the epidermal cilia and is thought to be an energy efficient mechanism for maintaining position

and continuous filter feeding (Stokes and Holland 1995). Adult lancelets may reach 6–9 cm in length (MacGinitie and MacGinitie 1949; Kozloff 1990; Stokes 1996; Riisgård and Svane 1999), depending on the species. *Branchiostoma floridae* adults can tolerate salinities down to 6‰ and temperatures from 3 to 37 °C. (Stokes and Holland 1996), in keeping with the large daily and seasonal environmental fluctuations in their preferred shallow sandy habitat.

In China, they are harvested for human food (MacGinitie and MacGinitie 1949; Kozloff 1990); a 35 metric ton harvest, representing about 1 billion individuals, was recorded by a single Chinese lancelet fishery (Ruppert and Barnes 1994). Adults are an important food item for bottom-feeding fish (Stokes and Holland 1996; Cabral et al. 2003) and small crustaceans (Stokes and Holland 1996). They undoubtedly form a portion of the diet of shorebirds; Ruppert and Barnes (1994) report that in Brazil farmers run flocks of chickens onto sandy shores so that the chickens can feed on them.

### Phylum Hemichordata

These deuterostomes, grouped with the protochordates, are all marine like the Tunicata. They are more closely related to echinoderms and, although they possess some chordate characters, they are phylogenetically considered far removed from the Chordata (Cameron et al. 2000). Hemichordates are common and widespread (Ruppert and Barnes 1994; Smith et al. 2003) but have been studied primarily for their chordate affinities as they relate to phylogenies rather than their ecology (Cameron 2005). There are two classes, the solitary enteropneust worms and the colonial pterobranchs. Enteropneusts (also called acorn worms) are deposit or suspension feeders (a nice description of hemichordate feeding methods is summarized in Ruppert and Barnes 1994); most species live in a burrow lined with mucus and are most common on shallow subtidal mud and sand flats, but they are also very abundant near many hydrothermal vents. With densities up to 200·m<sup>-3</sup> (Kozloff 1990), a significant portion of sediment on a flat may be moved through the digestive tracts and re-deposited on the surface every day. However, they have become rare in many areas of the US with the disappearance by development and dredging of all but a small fraction of natural tidal flats. Hedgpeth (1968) wrote that *Saccoglossus pusillus* (Ritter, 1902) was abundant in San Diego and Los Angeles, California, and Charleston, Oregon, in the first half of the 20th century but is rare or absent now. A few species are free-living under rocks and among seaweed holdfasts. There are a few deep-water species, some of which live near hydrothermal vents (Kozloff 1990; Ruppert and Barnes 1994). The largest species, *Balanoglossus gigas* Fr. Müller (Spengel, 1893), is more than a metre in length; most are less than 45 cm.

The epidermis, which is highly glandular, produces mucus but also bromine compounds that may be antibacterial, anti-competitive, or antipredator in function. High levels of a bromophenol in burrows of *Saccoglossus kowalevskii* (Agassiz, 1873) appeared to be toxic to aerobic bacteria (King 1988), although no appreciable microbial effects were reported by Steward et al. (1996). These bromophenols also accumulate in the processed sediments surrounding enteropneust burrows, where they may have a significant negative effect on recruitment of other taxa such as polychaete and

mollusc larvae (Woodin et al. 1997) or sand crabs (Sharief and Azariah 1997) to the infaunal community. Effects on the overall microbial community in the sediments owing to the removal of bacteria by deposit feeding, as well as the production of fecal castings, are probably short-lived (Plante and Wilde 2001; Wilde and Plante 2002). Predators include flatfish (Dou 1995) and blue stingray (Ebert and Cowley 2003), whose diets include up to 75% *Balanoglossus capensis* (Gilchrist, 1908) in nearshore waters in South Africa. However, *Ptychodera bahamensis* (Spengel, 1893) was found to be unpalatable to blue wrasse (Kicklighter et al. 2003) because of its chemical defense. The snail *Terebra dislocata* (Say, 1822) feeds on *Balanoglossus aurantiacus* (Girard, 1853) but takes only the posterior tip of the worm, a region easily broken off but also easily regenerated (Ruppert and Barnes 1994).

Unlike the Tunicata which are hermaphroditic, enteropneusts are dioecious. At least one species is viviparous, but most have external fertilization and development. In addition to sexual reproduction, some enteropneusts reproduce asexually by fragmentation. The ciliated echinoderm-like larva may be short-lived, nonfeeding, and simple in structure or (more usual) long-lived and planktotrophic. A recently discovered very small species produces a non-swimming juvenile that lives interstitially (Cameron 2002).

Pterobranch zooids are small, 5 mm or less in size, inhabit tubes interconnected by stolons, and filter-feed by means of ciliated tentacles on the oral arms. Only about 25 species are known, but because they are easily overlooked, this number is surely an underestimation. Reproduction is asexual by stolon budding or fragmentation, or sexual with a short-lived ciliated nonfeeding larva; pterobranchs are monoecious, although individual zooids are usually either male or female (Kozloff 1990). At least some species form a dedifferentiated overwintering stage (Dilly 1975). They occupy shallow water benthic surfaces such as coral rubble in warm-water areas, as well as deep-water areas worldwide including the Antarctic (Kozloff 1990). *Rhabdopleura* species have been collected down to at least 900 m (Stebbing 1970). Large numbers of *Rhabdopleura compacta* Hincks, 1880 inhabit the concave side of dead bivalve shells near Plymouth, England, and numerous invertebrates of several phyla are associated with them. Direct observation by SCUBA diving showed that because of hydrodynamic forces on the shells the concave side was always facing down (Stebbing 1970).

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