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Are kelp holdfasts islands on the ocean floor? – indication for temporarily closed aggregations of peracarid crustaceans

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Abstract

During the colonisation process of islands, newly immigrating species often arrive as single individuals. Islands that have received single colonisers may subsequently harbour large populations of a species, while other islands may completely lack this species. Exchange between islands is limited, thereby strongly affecting evolutionary processes. While this concept is widely used in the context of oceanic islands or habitat patches on the mainland, it is rarely used to explain and examine the distribution patterns of marine invertebrates. Benthic marine organisms inhabiting patches with island-like features may also be restricted in their movements between patches. Once established in a patch, it may be more favourable to remain there rather than moving to another patch. Juveniles of species with direct development may recruit to the island patch of their parents. Herein, we examined the peracarid fauna in patches that have island-like features, i.e. kelp holdfasts. The number of peracarid species within an individual holdfast increased with its size. Similarly, the number of individuals per holdfast increased with holdfast size. However, several peracarid species showed a strongly aggregated distribution pattern, being highly abundant in some holdfasts and almost completely absent in others. Our results suggest that these aggregations of conspecifics may be a consequence of the peracarid reproductive biology: fully developed juveniles emerge from the female's marsupium and recruit to the immediate vicinity of their mother, showing little or no tendency to emigrate towards other patches. At present, while it is not known how long peracarid aggregations within kelp holdfasts persist, our data suggest that some juveniles may remain with the natal holdfast and possibly reproduce therein. It is concluded that, during certain time periods, reproduction rates of peracarids in a holdfast may exceed their migration rates between holdfasts.

Introduction

Many marine microhabitats may have island-like characteristics and organisms inhabiting such microhabitats may, for certain time periods, be spatially isolated from conspecifics inhabiting other nearby microhabitats. Specifically, organisms may immigrate to or emigrate from these islands and, once established, may use them to conduct all their activities including feeding and reproduction. Founder effects may occur, particularly in well isolated microhabitats (=islands). Few individuals may reproduce and build an island population that has only limited exchange with neighbouring islands. These founder effects are well known from terrestrial species with individuals that reproduce and build local populations within a particular island or patch. In the marine environment, founder effects have received comparatively little attention, possibly because of the large proportion of species with planktonic larval stages. Reproductive isolation is considered less likely in these marine organisms than in terrestrial organisms since larvae (= gene-carrier) are easily transferred and exchanged between microhabitats. However, many marine invertebrates such as polychaetes, molluscs, echinoderms and crustaceans have direct development. For example, snapping shrimp release their offspring within their sponge colony and juveniles of several species remain therein, forming large colonies of closely related individuals (Duffy, 1996; Duffy & Macdonald, 1999). Another group of crustaceans without any free-living larval stages is the peracarids. Peracarid species are common inhabitants of many marine microhabitats such as sponges, pieces of wood, corals and macroalgae. Development in peracarids is direct and it is increasingly recognised that juveniles may recruit to the immediate vicinity of their parents (Flach, 1992; Thiel, 1999). Single ovigerous females immigrating into a patch may potentially be able to serve as founders for large aggregations of closely related individuals within one microhabitat island. Reproductive females, when present in a patch, may be able to sustain a local group, while in patches without reproductive females, a species may disappear quickly unless it is repeatedly replenished by newly immigrating individuals. When reproduction rates in a patch are not sufficiently high to counterbalance losses due to death and migration, local populations within a patch may become extinguished (see e.g. Gunnill, 1982, 1983).

Several marine microhabitats have island-like features, such as sponges, ascidians, corals, mangrove trees and macroalgae. Herein, we examined whether distinct peracarid aggregations occur in holdfasts of three common kelp species along the Chilean coast.

Materials and methods

Macroalgae, *Lessonia trabeculata*, *L. nigrescens* and *Macrocystis integrifolia,* were sampled during the austral fall (April 1999) in the shallow subtidal zone around Punta de Choros, Chile (29.25 S, 71.55 W) (Fig. 1). The algal density in the kelp beds was determined by transect and quadrat counts. For *L. trabeculata* and *M. integrifolia*, all plants in 2 m-wide and 10 m-long transect strips were counted (10 strips counted for each species). For *L. nigrescens,* all plants in 17 randomly chosen quadrats (1 m^2) were counted.

Thirty-one individual plants of *L. trabeculata*, 36 of *L. nigrescens* and 27 plants of *M. integrifolia* were collected at the respective sampling sites (Fig. 1). Plants of *L. trabeculata* and *M. integrifolia* were collected 7–10 m below MLW (mean low water), and plants of *M. nigrescens* in the low intertidal zone. Whole plants were separated from the substratum and stored immediately in mesh bags (1 mm mesh diameter). On the shore, whole plants were placed in large trays and the blades separated from the holdfasts. For preservation and subsequent transport to the laboratory, each holdfast, together with all associated macroinvertebrates, was placed in a large sealable plastic bag and formalin was added until a 10% solution was achieved. In the laboratory, holdfasts were carefully retrieved from the bag and washed over large trays with freshwater. Holdfasts were dissected and surveyed carefully for macrofauna organisms. The contents remaining in the trays and bags were washed over a 0.5 mm sieve, which retained all remaining macrofauna organisms. All macrofauna was sorted from the residue and identified to the lowest taxonomic level. Herein, we distinguish two main groups: the non-peracarid macroinvertebrates and the peracarid macroinvertebrates (amphipods, isopods and tanaids). The total volume of the kelp holdfasts was determined by placing all holdfast pieces in a beaker and measuring the volume of water displaced. Previous studies had revealed that holdfast volume is best suited to describe species abundance and diversity in kelp holdfasts (Vásquez & Santelices, 1984). The relationship between holdfast volume and the species composition was examined by a regression analysis searching for the curve that best fitted the data (utilizing the program SYSTAT8.0).

Results

The average density of kelp plants was 3.7 (± 0.61 SE) plants m^{-2} (*Lessonia nigrescens*), 3.5 (± 0.30 SE) (*Macrocystis integrifolia*) and 2.1 (± 0.25 SE) plants m^{-2} (*Lessonia trabeculata*). The number of invertebrate species per kelp holdfast was strongly correlated with the volume of the holdfast, both for other macroinvertebrates and for peracarids (Fig. 2). The number of other macroinvertebrate species increased rapidly in small and medium-sized holdfasts but appeared to approach an equilibrium in larger holdfasts. The number of peracarid species increased over the whole size range of holdfasts of *L. trabeculata* and *M. integrifolia* (Fig. 2). Some holdfasts harboured comparatively large numbers of peracarids, but holdfasts of similar sizes contained only few individuals.

Many peracarid species occurred exclusively within the holdfasts of one algal species (Table 1). The most common species was the boring amphipod *Perampithoe femorata,* which occurred in about 70% of all samples. The suspension feeding amphipod *Aora typica* occurred in about 40% of all samples. The only other species that were found in holdfasts of all three algal species were the amphipods *Ericthonius brasiliensis*, *Gammaropsis typica*, *Ventojassa frequens* and *Maera incerta*. Many isopod and tanaid species were found only in holdfasts of one algal species.

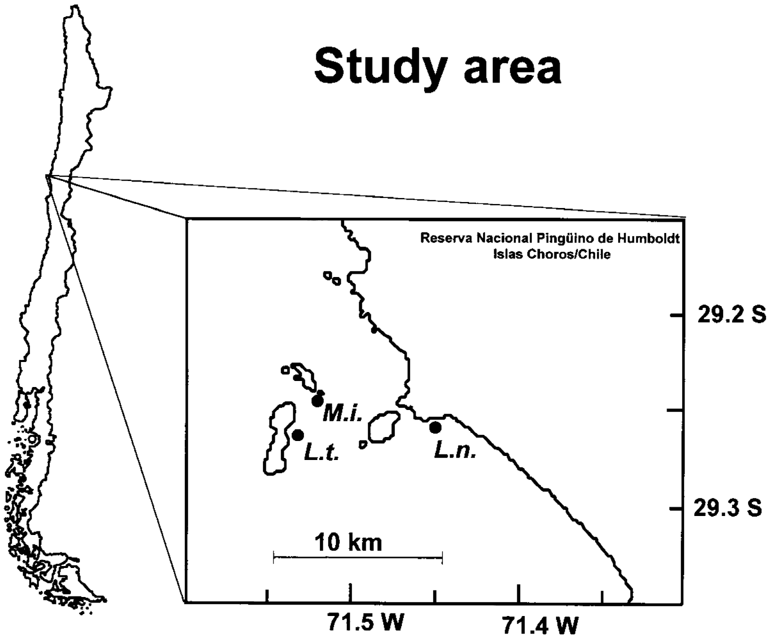

Figure 1. Study area at the northern-central coast of Chile showing sites of collection for individual plants of the macroalgae *Lessonia trabeculata* (*L.t.*), *L. nigrescens* (*L.n.*), and *Macrocystis integrifolia* (*M.i.*) during the austral fall (April 1999).

For most of the common invertebrate species, the number of individuals was significantly correlated with the volume of the holdfasts (Fig. 3). In particular, species with pelagic larvae (*Brachidontes granulata, Semimytilus algosus,* Nereidae sp., Nemertea sp., *Parantheopsis cruentata*) or with highly mobile adults (*Pachycheles grossimanus, Gaudichaudia gaudichaudi*) occurred in densities related to the volume of the holdfasts. This trend was less clear for the most abundant peracarid species. These appeared to occur in similar numbers in holdfasts of all sizes (see e.g. *Perampithoe femorata* and *Aora typica* in Figure 4). However, there were always a few holdfasts in which unusually high numbers of individuals occurred (Fig. 4). For example, most holdfasts contained only a few individuals of the tube-building amphipod *Ericthonius brasiliensis,* but there were a few holdfasts with > 20 individuals per holdfast (Fig. 4). Similarly, for the amphipods *Leucothoe* sp. A and *Ventojassa frequens,* most holdfasts contained between 0 and 5 individuals, but a few harboured > 20 individuals per holdfast. In most cases, the typical clutch size of these species ranged between 10 and 30 individuals (see shaded areas in Figure 4). This suggests that, in holdfasts with high numbers of individuals, females had released offspring that had established subsequently in those holdfasts.

Discussion

The number of macroinvertebrate species and individuals per holdfast was correlated with holdfast volume. An increase of individuals per holdfast with increasing holdfast volume was found for single macroinvertebrate species that recruit to holdfasts as larvae and that remain mobile throughout their adult life. A different distribution pattern was found for many common peracarid species. On several occasions, dense peracarid aggregations were found in the kelp holdfasts that did not correspond to the holdfast size. Some holdfasts harboured large numbers of conspecifics, while others contained only single individuals. These aggregations could indicate that juvenile peracarids recruit to their natal holdfast.

Macroinvertebrates in kelp holdfasts

Kelp holdfasts represent an important microhabitat for a variety of macroinvertebrates (Vásquez & Santelices, 1984; Moore, 1986; Smith & Simpson, 1992). Inhabitants of kelp holdfasts receive shelter from predation (Cancino & Santelices, 1984) and access to food and mates (Dayton, 1985; Tegner et al., 1995). Most species are not associated exclusively with holdfasts, and occur also in surrounding habitats under cobble stones, on rock surfaces, or on other secondary sub-

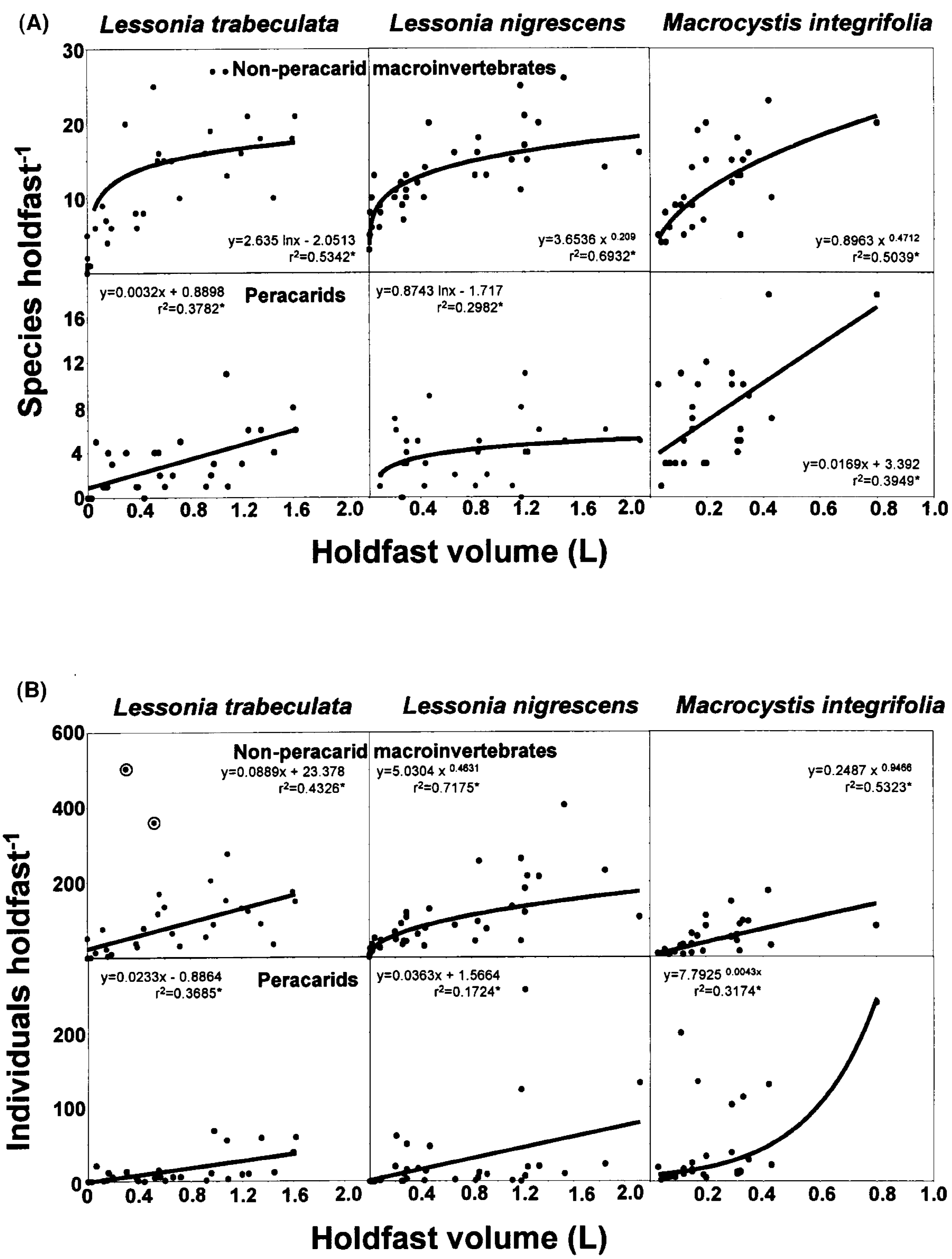

Figure 2. Relationship between holdfast volume and (A) number of species and (B) number of individuals for non-peracarid and peracarid macroinvertebrates found in *Lessonia trabeculata, L. nigrescens* and *Macrocystis integrifolia*; *n* = 31 holdfasts of *L. trabeculata*, 36 holdfasts of *L. nigrescens* and 27 of *M. integrifolia* were analysed; regression equations are based on units of ml.

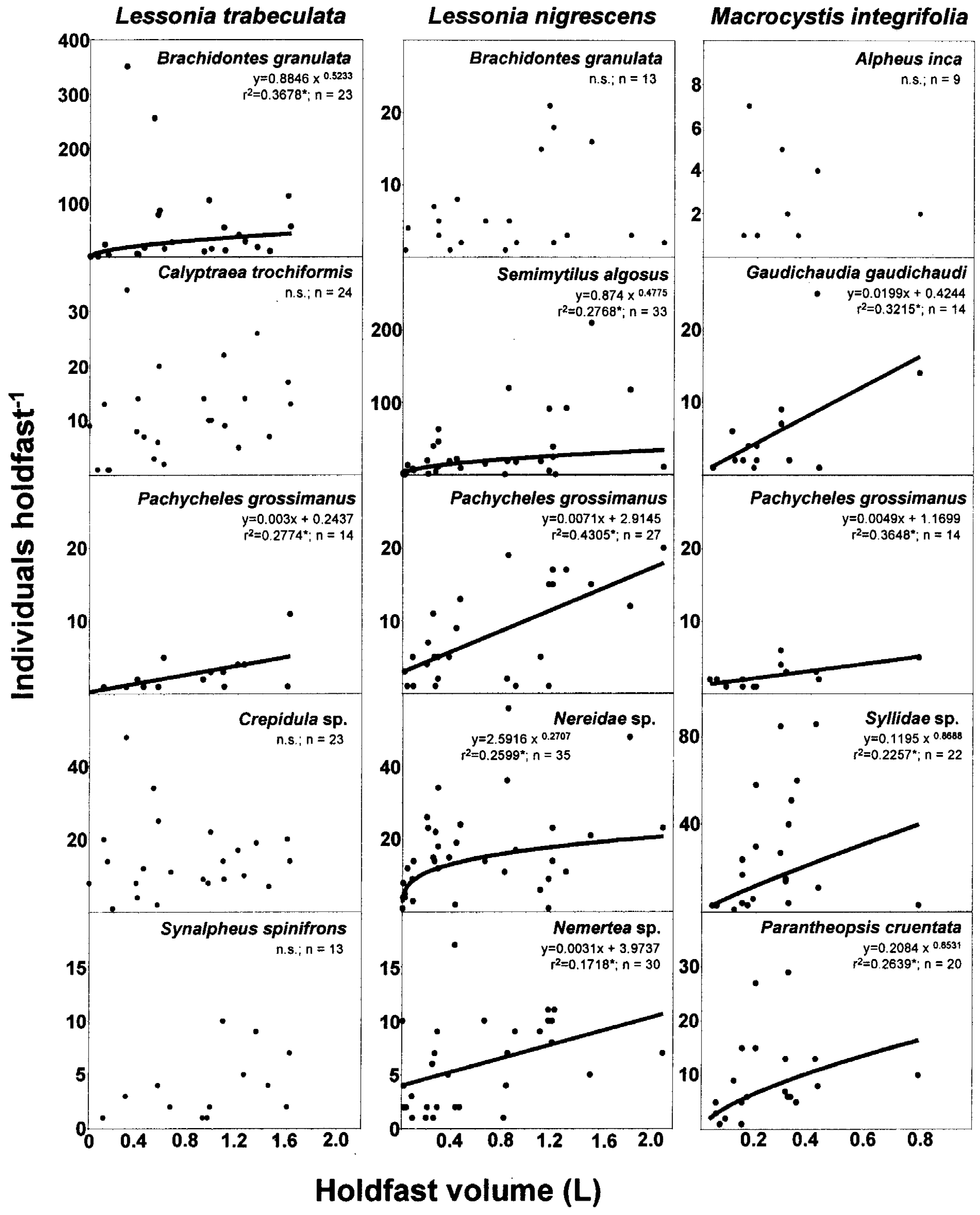

Figure 3. Relationship between holdfast volume and number of individuals for the most common non-peracarid macroinvertebrates found in *Lessonia trabeculata*, *L. nigrescens*, and *Macrocystis integrifolia*; *n* = number of holdfasts in which the respective macroinvertebrate species was found – only these holdfasts were used for the regression analysis; regression equations are based on units of ml.

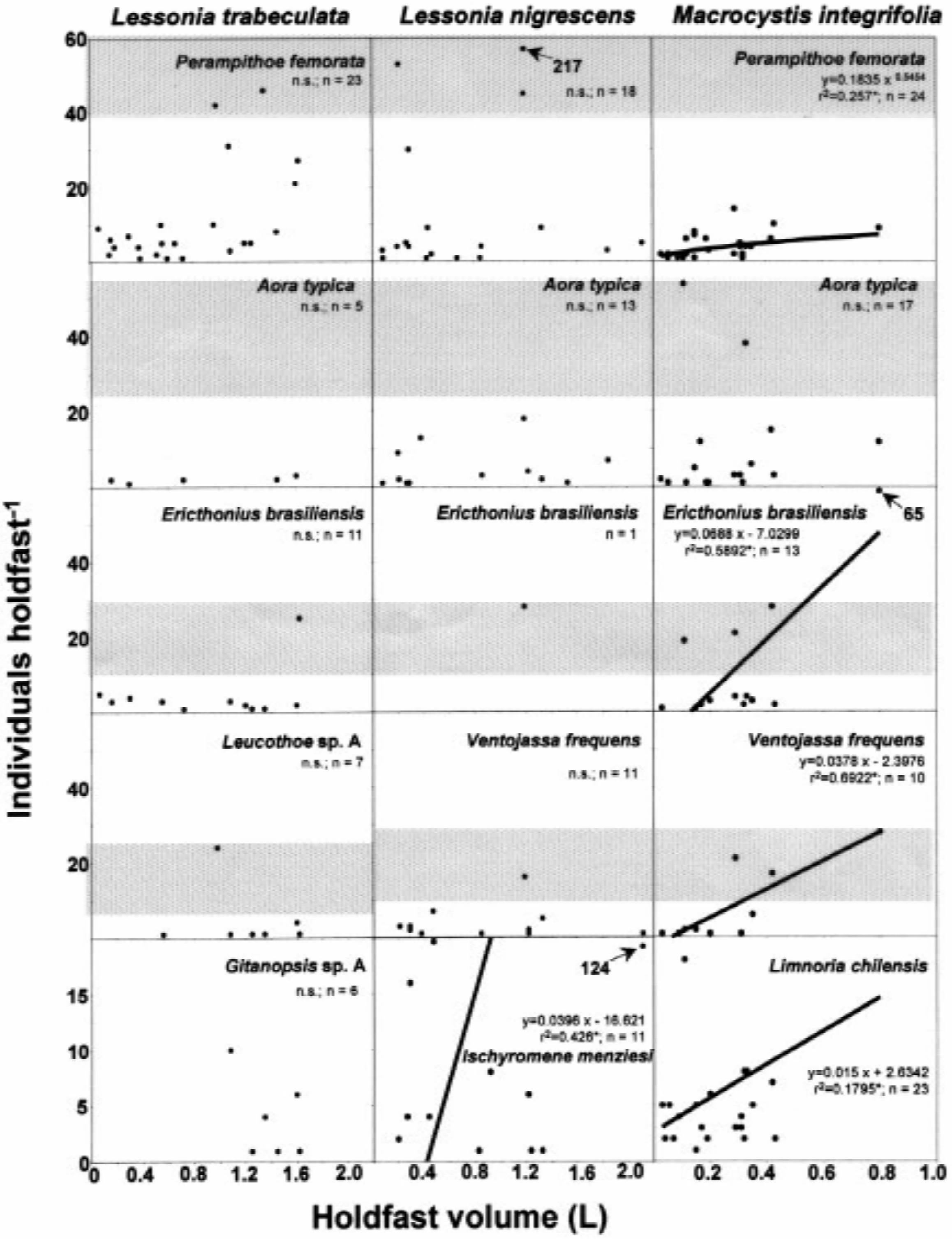

Figure 4. Relationship between holdfast volume and number of individuals for the most common peracarid macroinvertebrates found in *Lessonia trabeculata*, *L. nigrescens*, and *Macrocystis integrifolia*; *n* = number of holdfasts in which the respective peracarid species was found - only these holdfasts were used for the regression analysis; shaded areas indicate typical clutch sizes for the species for which information was available (own data and from Sainte-Marie, 1991); regression equations are based on units of ml.

Table 1. Percentage of samples in which the respective peracaid species occurred.

	Functional group	Taxon	*Lessonia trabeculata*	*Lessonia nigrescens*	*Macrocystis integrifolia*
			n = 31	*n* = 36	*n* = 27
Aora typica	s	a	16.1	36.1	63.0
Aora sp. A	s	a			11.1
Ericthonius brasiliensis	s	a	35.5	2.8	48.1
Ischyrocerus longimanus	s	a	12.9		22.2
Gammaropsis typica	s	a	6.5	2.8	25.9
Gammaropsis typica, var. Y	s	a			3.7
Gammaropsis sp. A	s	a		8.3	3.7
Ventojassa frequens	s	a	25.8	30.6	37.0
Ampelisca sp. A	s	a			11.1
Corophium sp. A	s	a	3.2		
Caprella equilibra	s	a	12.9		7.4
Caprella sp. A	s	a	3.2		
Caprella penantis	s	a	3.2		3.7
Tanais (marmoratus)	s	t		19.4	
Tanaid sp. B	s	t		8.3	
Tanaid sp. C	s	t	3.2		22.2
Hyale hirtipalma	g	a		19.4	3.7
Hyale (grandicornis)	g	a		2.8	
Ianiropsis (chilensis)	g	i	9.7	25.0	
Joeropsis bidens	g	i		47.2	14.8
Santia dimorphis	g	i		5.6	
Amphoroidea typa	g	i	3.2	5.6	
Ischyromene menziesi	g	i		30.6	
Cymodocella foveolata	g	i		13.9	
Perampithoe femorata	b	a	74.2	50.0	88.9
Bircenna fulva	b	a			29.6
Limnoria chilensis	b	i			85.2
Elasmopus chilensis	?	a	9.7		55.6
Elasmopus sp. A	?	a	3.2		11.1
Stenothoe sp. A	?	a	12.9		
Lysianassa sp. A	?	a			7.4
Leucothoe sp. A	?	a	22.6		
Paramoera sp. A	?	a			59.3
Maera incerta	?	a	9.7	8.3	44.4
Melita inaequistylis	?	a			37.0
Gitanopsis sp. A	?	a	19.4		
unidentified amphipod	?	a			22.2

s – suspension-feeder; g – grazer; b – borer; a – amphipod; i – isopod; t – tanaid.

strata such as sponges and ascidians (e.g. Cancino & Santelices, 1984). In the present study, we found that both the number of species and the number of individuals increased with holdfast volume. While the number of species of other macroinvertebrates appeared to reach an equilibrium in the largest holdfasts, the number of individuals continued to increase even in the largest holdfasts (see also Vásquez & Santelices, 1984). For sponges, Westinga & Hoetjes (1981) found similar results, with the number of invertebrate taxa increasing logarithmically with sponge volume (reaching an equilibrium) and the total number of individuals being directly proportional to sponge volume (not reaching an equilibrium). Based on these results, the authors concluded that “the intra-sponge-fauna indeed is an ecological community, in which, however, interrelationships are not yet clear.” A similar conclusion can be drawn for the fauna inhabiting kelp holdfast as is suggested by the distinct relationship between microhabitat characteristics (here: holdfast volume) and the number of species and individuals inhabiting individual holdfasts. However, little is known about the general biology of many of the macroinvertebrates inhabiting the holdfasts, let alone the biotic interactions among them.

Peracarid aggregations in kelp holdfasts

The peracarid crustaceans inhabiting kelp holdfasts comprise a variety of functional groups such as grazing, boring and suspension feeding species, and possibly predators and scavengers. All peracarid species share a common reproductive feature – the female brood pouch from which fully developed juveniles emerge. After becoming independent from their parents, these juveniles are capable of establishing a home (e.g. a tube or a burrow) and feeding in a way similar to the adults. Several studies have indicated that juvenile amphipods may recruit in the immediate vicinity of their parents (Flach, 1992; Thiel et al., 1997). Similarly, it has been observed that juveniles of kelp-boring amphipods and isopods excavate their burrows as offshoots of the parental burrow (Menzies, 1957; Jones, 1971; Conlan & Bousfield, 1982; Conlan & Chess, 1992). Aggregations of conspecifics may thus be a consequence of the reproductive biology of peracarids, yet it is not known how long these aggregations persist. In situations where juvenile individuals find themselves released into a suitable microhabitat, they may remain therein without any intention of leaving. Many peracarids inhabiting kelp holdfasts are boring and suspension feeding species that have a relatively sedentary life style associated with tubes or burrows. Duffy & Hay (1994) found that a tube-dwelling amphipod was much less mobile than a free-living species. Several studies of soft-bottom dwelling amphipods indicate that emigration rates are low in disturbance-free environments but substantially increase when disturbers are present (Flach & De Bruin, 1994). While most of the species found in the present study are potentially good swimmers, they may not leave their natal kelp holdfast if not disturbed by conspecifics or benthic predators. Furthermore, fish predation on peracarids is high in the shallow coastal waters of the central Chilean coast (Muñoz & Ojeda, 1997, 1998) and it is, therefore, unlikely that peracarids voluntarily leave the shelter of a kelp holdfast.

While the above considerations suggest that many peracarids remain in the natal holdfast if conditions are favourable, other studies on algal-dwelling peracarids indicate that they are highly mobile. Studies on epifaunal amphipods inhabiting the algal canopy indicated a high turnover of individuals within time periods of days (Edgar, 1992; Taylor, 1998), thus indicating that individuals may easily move from one plant to another. Epifaunal peracarids that forage on algal fronds may be highly mobile, moving easily between algae that provide food and those that offer shelter (e.g. Buschmann, 1990). In contrast to these epifaunal amphipods, species that inhabit holdfasts may find both food and shelter in these microhabitats, thus having little need to change their location.

Do the aggregations represent closely related individuals? The fact that peracarid crustaceans may recruit in the immediate vicinity of their parents suggests that on a small scale (here: within individual holdfasts), some individuals are closely related to each other. Our data suggest that, for certain time periods (weeks to months), holdfasts may harbour aggregations of closely related individuals. A consequence of this ‘neighbourhood recruitment’ would be high genetic variation over relatively small distances (several m, e.g. between holdfasts). Unfortunately, we are not aware of any studies on marine invertebrates addressing the question of genetic variation over these small distances (but for marine plants see e.g. Reusch et al., 1999). There are, however, several molecular studies on amphipod populations within bay systems that indicate high genetic variation between individuals separated by distances of only a few km (Stanhope, 1993; Wilson et al., 1997). The main cause for this high genetic variation could be the fact that amphipods have direct development and that juveniles establish home in the vicinity of their parents. Studies on other crustaceans and a gastropod with direct development also revealed high genetic variation over similar distances (Knight et al., 1987; Johannesson et al., 1993; Duffy, 1996). Poulin & Féral (1995) found dense aggregations of the brood-protecting echinoid *Abatus cordatus* that has direct development - juveniles immediately recruit to the patch they were born in. The authors hypothesize that patches may remain stable for several years, resulting in individuals within a patch being more closely related to each other than those between patches (Poulin & Féral, 1994, 1998). While these studies have not addressed the question of genetic variation over even smaller distances (several m), they indicate that, in marine invertebrates with direct development, high genetic variation may occur over surprisingly small distances. In contrast, comparatively low genetic variation was found on similar spatial scales for marine molluscs with indirect development and a pelagic larval phase (De Wolf et al., 1998; Skalamera et al., 1999). Since most amphipod and other peracarid species are relatively mobile, aggregations of closely related individuals may not be stable for very long time periods. However, during certain time periods, migration rates may be strongly exceeded by reproduction rates within individual holdfasts. We suggest that aggregations of peracarids in holdfasts may occasionally persist sufficiently long for siblings to attain sexual maturity. As a consequence, the likelihood that closely related individuals mate in these holdfasts (and other biotic microhabitats) would be high. It is not known whether abnormalities found in typical algal dwelling amphipods (e.g. Vader, 1968; Moore, 1973) are a consequence of inbreeding in island-like algal patches. Molecular and experimental studies are required to confirm our suspicion that temporarily closed aggregations of peracarids occur in kelp holdfasts and other biotic microhabitats such as sponges, ascidians or wood.

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