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Cleaner Fish: from Mutualism to Parasitism – or vice versa?

Putzerfische: vom Mutualismus zum Parasitismus – oder umgekehrt?

C. Dieter Zander
Zoologisches Institut, Universität Hamburg, Martin-Luther-King-Platz 3,
20146 Hamburg-Rotherbaum, Germany, cedezet@uni-hamburg.de

Summary: Based on the cleaner-client relationship mutualism is here discussed as a pattern of symbiosis. The question is whether mutualism arose from commensalism and led finally to parasitism or arose from parasitism. The main cleaner fish around the world belong to the families Echineidae, Gobiidae, Chaetodontidae and mainly Labridae. Additionally, many labrid juveniles are facultative cleaners. The most known cleaner species is *Labroides dimidiatus* from the Indo-Westpacific. The cleaner symbiosis may have been derived from narrow body contacts of different fish species as occur in many feeding communities. Additionally, several labrid cleaner species are also occasional parasites, which feed sometimes on skin and parts of fins of their clients. *Labroides* species from Hawaii are even predominantly parasites. In the Indo-Westpacific fang-blennies (Blenniidae), a group which presents no cleaner species, imitate the coloration of *L. dimidiatus*. In the freshwater of River Danube several Cyprinidae are cleaning one another, a status which can be considered as a first step to become a main cleaner species. Therefore, there are arguments that cleaner mutualism has evolved from commensalism as well as from parasitism.

Key words: Cleaner fish, geographical distribution, symbioses, direction of evolution

Zusammenfassung: Die Frage, ob der Mutualismus vom Kommensalismus ausgehend entstanden ist und letztendlich zum Parasitismus führte oder sich direkt vom Parasitismus her entwickelt hat, wird anhand der Symbiose von Putzerfischen und ihren Kunden diskutiert. Die Haupt-Putzerfische in verschiedenen Regionen der Welt stammen aus den Familien Echineidae, Gobiidae, Chaetodontidae und überwiegend aus den Labridae. Zudem sind viele Jungfische von Labriden-Arten fakultative Putzer.. Am bekanntesten ist *Labroides dimidiatus* aus dem tropischen Indo-Westpazifik. Die Putzersymbiose könnte ihren Ursprung von engen Körperkontakten verschiedenartiger Fischarten haben, wie sie bei Mitgliedern von Fressgemeinschaften häufig auftreten. Andererseits haben sich einige Putzer-Lippfische auch als gelegentliche Parasiten erwiesen, da sie zusätzlich auch Haut und Flossenteile ihrer Klienten aufnehmen. In Hawaii gibt es sogar *Labroides*-Arten, die sich überwiegend parasitisch ernähren. Im Indo-Westpazifik ahmen parasitische Säbelzahn-Schleimfische (Blenniidae) die Färbung von *L. dimidiatus* nach; aus dieser Gruppe sind aber keine Putzer bekannt. Die Beziehungen im Süßwasser der Donau, wo mehrere Cyprinidae-Arten sich gegenseitig putzen, können als eine Vorstufe der Lebensweise eines Hauptputzers vermutet werden. Damit gibt es Argumente, dass Putzerfisch-Mutualismus vielleicht sowohl aus Kommensalismus als auch Parasitismus entstanden sein könnte.

Schlüsselwörter: Putzerfische, geografische Verbreitung, Symbiosen, Richtung der Evolution

1. Introduction

Mutualism and parasitism are two modes of symbiosis, of which definition by DE BARY (1879) means the living together of organisms of different species. In symbiosis this author included several associations, ranging continuously from commensalism, which favors only one partner, over a mutualistic partnership with benefit to both partners, to parasitism which benefits one partner and disadvantages the other. One way of such an evolution may have originated from parasitism, e.g. in the case of endosymbiosis in plants (MEREZHKOWSKY 1905;

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Wallin 1927; Margulis 1970). In contrast, animal endoparasites live in body cavities of other metazoans, such as free living turbellarian platyhelminths that entered as commensals gill cavities of fish and crayfish hosts and are assumed to evolve by this way to endoparasitic groups of platyhelminths (Price 1980). Ectoparasitism may have developed from animals which use the hosts as vehicles in order to attain comfortable habitat changes. This was the way which many crustaceans have persuaded onto skin or fins of fish prior to become parasites (Costello 1991; Treasurer 1993).

Since the description by Eibl-Eibesfeldt (1955) the cleaner symbiosis was an outstanding example for mutualism. This author observed the gobiid *Gobiosoma* spp. in the Caribbean, which pick off parasitic crustaceans from skin and fins of other fish species. Most research on cleaner fish was done on the labrid *Labroides dimidiatus* from the Indo-Westpacific. The cleaner profits by getting prey, the host profits from the loss of blood sucking parasites. This view on cleaner mutualism had been changed when Gorlick (1980) detected that the gut of the cleaner fish *Labroides phthirophagus* from Hawaii was filled with more mucus of fish than with parasitic crustaceans.

Therefore, the following compilation of results regarding cleaner fish observations from different areas of the world may contribute to the question, whether the cleaning symbiosis may be derived from commensalism or parasitism. An important pattern is the so called international cleaner dress which is presented by *Echineis naucrates*: a blue stripe along a light body.

2. Methods

For the following text and table 1 cleaner and parasite fish are classified to self created categories:
main cleaner – species which dominate as cleaner,
facultative cleaner – species which support main cleaners, mostly young individuals,
occasional cleaner – species which feed on other organisms than parasites as main food,
main parasites – species which feed predominantly on mucus or scales of other fish,
occasional parasites – species which are cleaner but sometimes behave as parasites.

3. Results

3.1. Circumtropical distribution

Echineis naucrates (Echineidae) (fig. 1a) is found in oceans around the world. This species presents a coloration which is model and imitated by several other cleaner fish, e.g. by the labrid *Labroides dimidiatus* or by the gobiids *Gobiosoma oceanops* and *G. evelynae*, but also by the parasitic *Aspidontus taeniatus* (Blenniidae) (Eibl-Eibesfeldt 1959).

Fig. 1: Representatives of cleaner fish around the world. **a** *Echineis naucrates* (Echineidae) is distributed in all seas of the tropic regions. Its coloration may be the model for several other cleaner fish species. **b** *Ctenolabrus rupestris* (Labridae) is a facultative cleaner in the North-East Atlantic. The dark spot on the tail may be the signal to be recognized by clients. **c** *Symphodus melanocercus* (Labridae) (here persuading a *Chromis chromis*) is a main cleaner in the Mediterranean Sea; its black tail mark is acknowledged by clients. **d** Young *Coris julis* (Labridae) are facultative cleaners; their characteristic coloration is similar to *E. naucrates* but with a brown horizontal line instead of a dark blue one. **e** *Labroides dimidiatus* (Labridae) (here with its client *Scolopsis ghanam*) is the main cleaner in the Indo-West-Pacific and imitator of the characteristic cleaner coloration of *E. naucrates*. **f** Young *Larabicus quadrilineatus* (Labridae) are facultative cleaners in the Red Sea. The bright blue body coloration differs slightly from that of *E. naucrates* (Photo: R. Gramckow). **g** *Johnrandallia nigrirostris* (Chaetodontidae) is main cleaner in the Galapagos-Archipelago. **h** *Gobiosoma evelynae* (Gobiidae) is one of main cleaner fish in the Caribbean Sea, its coloration is in accordance with the characteristic cleaner uniform.
Abb. 1: Einige Repräsentanten der Putzerfisch-Gilde aus der ganzen Welt. **a** *Echineis naucrates* (Echineidae) kommt in allen tropischen Meeren vor. Seine Färbung ist das Vorbild für viele andere Putzerfisch-Arten. **b** *Ctenolabrus rupestris* (Labridae) ist fakultativer Putzer im Nord-Ost-Atlantik. Der schwarze Fleck an der

Schwanzwurzel mag das entscheidende Signal für potenzielle Kunden sein. **c** *Symphodus melanocercus* (Labridae) ist der Hauptputzer im Mittelmeer. An der schwarzen Schwanzmarkierung wird er von seinen Kunden erkannt. **d** Jungfische von *Coris julis* (Labridae) sind fakultative Putzer, seine Färbung ähnelt der von *E. naucrates*, allerdings ist das dunkle Längsband braun. **e** *Labroides dimidiatus* (Labridae) (hier mit *Scolopsis ghanam*) ist der Hauptputzer im Indo-Westpazifik und ahmt die Färbung von *E. naucrates* nach. **f** Jungfische von *Larabicus quadrilineatus* (Labridae) putzen fakultativ im Roten Meer. Die hellblaue Körperfärbung weicht geringfügig von der des Vorbilds *E. naucrates* ab (Foto: R. Gramcko). **g** *Johnrandallia nigrirostris* (Chaetodontidae) ist der Hauptputzer im Galapagos-Archipel. **h** *Gobiosoma evelynae* (Gobiidae) ist einer der Hauptputzer in der Karibik, seine Färbung gleicht der charakterischen Putzertracht von *E. naucrates*.

3.2. Northeast Atlantic, including North Sea

Here the labrid *Ctenolabrus rupestris* is a facultative cleaner, which is often used in salmon farms in order to free these fish from parasitic copepods (Costello 1991; Treasurer 1993). Its coloration is not remarkable with exception of a black spot on the tail (fig. 1b). Additionally, young of several larger *Labrus* and *Symphodus* spp. (Labridae) are occasional cleaners. No parasite fish feeding on mucus and skin of other fish are known from this region.

3.3. Mediterranean Sea

In this region the small labrid *Symphodus melanocercus* (fig. 1c) is the main cleaner (von Wahlert & von Wahlert 1961; Zander & Nieder 1997; Zander et al. 1999), supported by young of the labrids *Coris julis* (fig. 1d) and *Thalassoma pavo*. Young *C. julis* have similar colorations as *E. naucrates* except that the longitudinal stripes are brown, young *T. pavo* have dark brown patterns on the sides, whereas *S. melanocercus* is conspicuous by a black marking on the tail which functions as signal for clients. Juveniles of several other *Symphodus* spp. were observed to clean occasionally. Cardinal fish (*Apogon imberbis*) are exclusively cleaned by young *Coris julis*, morays (*Muraena helena*), however, only by shrimps. Exclusive parasitic behavior of any fish species was not observed in this region. Evidently, *S. melanocercus* feeds on benthos, sometimes on plankton and is an occasional parasite (fig. 2, Detloff et al. 2010).

3.4. Subtropical East-Atlantic (Acores, Madeira, Canaries)

Surprisingly, in this region no main cleaner fish is present. Facultative cleaners are the young of the labrids *T. pavo* and *C. julis* such as in the Mediterranean. Also shrimps have a greater importance as cleaners than fish in this region (van Tassell et al. 1994; Wirtz 1995). In eastern Atlantic archipelagos no parasitic fish was observed until now.

3.5. Red Sea and West-Indopacific

In this wide area the labrid *Labroides dimidiatus* (fig. 1e) dominates as cleaner (Eibl-Eibesfeldt 1959). It imitates the worldwide cleaner coloration as do the facultative cleaner *L. bicolor* and *Thalassoma amblycephalus*. Young *Larabicus quadrilineatus,* which are endemic and facultative cleaner in the Red Sea, differ somewhat by coloration in that the body is bluish (fig. 1f). Unexpectedly, young individuals of the chaetodontid *Heniochus acuminatus* are facultative cleaners. In this region the parasite fang blenny *A. taeniatus*, whose coloration resembles that of *L. dimidiatus* (Eibl-Eibesfeldt 1959), is abundant. This camouflage confuses potential hosts of cleaners so that the parasite can approach the client and prey on pieces of skin and fins. The fang blenny *Plagiotremus rhinorhynchus* behaves in a similar way but its coloration differs by its broken blue line from the model (Zander 2017). On the other side, Grutter (1996) observed that *L. dimidiatus* feeds in the

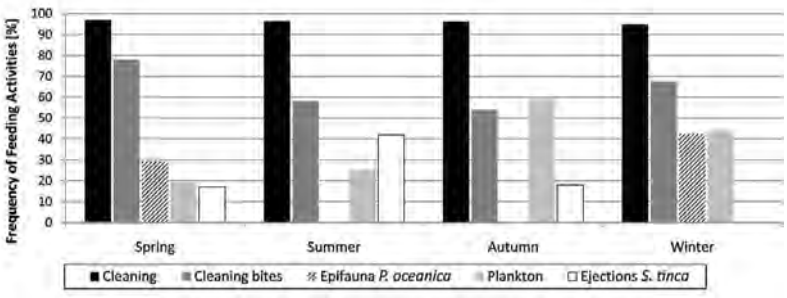

Fig. 2: Frequency of seasonal feeding activities of *Symphodus melanocercus* (from Detloff et al. 2010).
Abb. 2: Fressaktivität (Frequenzen) von *Symphodus melanocercus* im Jahresverlauf (aus Detloff et al. 2010).

Great Barrier Reef not only on parasites but also on skin from their clients therefore, it is an occasional parasite.

3.6. East Pacific (Galapagos, Hawaii)

Surprisingly, in Galapagos main cleaner is neither a labrid nor a gobiid. Main cleaners are beside *E. naucrates* (cleans large clients) the chaetodontid *Johnrandallia nigrirostris* (fig. 1g). Young of the labrids *Bodianus diplotaenia* and *Thalassoma lucasanum* as well as adults of the small-sized gobiid *Gobiosoma digueti* clean occasionally. In Hawaii prevails a special situation, because the endemic *Labroides phthiriphagus* is more parasite than occasional cleaner (Gorlick 1980). Other parasites are several *Plagiotremus* spp., but occasional cleaner in Hawaii are adult and young *Thalassoma duperrey*.

3.7. Caribbean

Main cleaners are the gobiids *Gobiosoma evelynae* (fig. 1h) and *Gobiosoma oceanops*, which present the characteristic cleaner coloration of *E. naucrates* and *L. dimidiatus*. In this area the cleaner symbiosis was at first at all observed by Eibl-Eibesfeldt (1955). Several young labrids like *Thalassoma bifasciatum* or young pomacanthids like *Paracanthus paru* are facultative cleaners.

3.8. Freshwater Europe

Only few occasional observations are known from fresh waters In the River Danube, Abel (1971) observed that *Scardinius erythrophthalmus* has a central position, because it cleans *Alburnus alburnus*, *Tinca tinca, Rutilus rutilus* and conspecifics, but is cleaned itself by *A. alburnus* and

Tab. 1: Compilation of known cleaners and parasitic fish in diverse regions of the world. Compiled according to the cited literature.
Tab. 1: Zusammenstellung bekannter Putzer und parasitischer Fische aus verschiedenen Regionen der Welt. Zusammengestellt nach der genannten Literatur.

	Main cleaner	Facultative cleaner	Occasional cleaner	Parasites	Occasional parasites
Nordeast-Atlantik/North Sea		*Ctenolabrus rupestris*	*Labrus* spp. juv *Symphodus* spp. juv.		
Mediterranean Sea	*Symphodus melanocercus*	*Coris julis* juv. *Thalassoma pavo* juv.	*Symphodus* spp. juv		*Symphodus melanocercus*
Subtropical East-Atlantik Acores, Madeira, Canary archipelagos		*Thalassoma pavo* juv. *Coris julis* juv.			
Tropical East-Atlantik Cap Verde	*Echineis naucrates*	*Thalassoma pavo* juv. *Holocanthus africanus* juv.			
Red Sea, Indo-Westpazifik	*Echineis naucrates* *Labroides dimidiatus*	*Labroides bicolor* *Larabicus quadrilineatus* juv. *Thalassoma amblycephalus* juv. *Heniochus acuminatus juv.*		*Aspidontus taeniatus* *Plagiotremus rhinorhynchus*	*Labroides dimidiatus*
Eastpazific Galapagos, Hawaii	*Echineis naucrates* *Johnrandallia nigrirostris*	*Gobiosoma digueti* *Bodianus diplotenia juv.* *Thalassoma lucasanum juv.*	*Labroides phthiriphagus*	*Labroides phthiriphagus* *Plagiotremus azalea* P. ewaensis *P. gosline*	
Caribbean Sea	*Echineis naucrates* *Gobiosoma evelynae* *Gobiosoma oceanops*	*Thalassoma bifasciatus juv.* *Pomacnthus paru juv.*			
Fresh water Europe Danube River		*Rhodeus amarus* *Scardinius erythrophthalmus* *Alburnus alburnus* *Rutilus rutilus* *Tinca tinca*	*Perca fluviatilus* juv.		

Rhodeus sericeus. *R. rutilus* probably cleans *Perca fluviatilis* that cleans also conspecifics. Intraspecific cleaning is generally characteristic within this fish assemblage.

4. Discussion

The most noteworthy results of the present article are: 1) the coloration of cleaner fish is a signal for their clients. 2) Changes from a cleaning to a parasitic way of life are flowing; several facts give evidence for an origin of cleaning symbioses from commensalism as well as from parasitism

At most, labrids take over the role as main cleaner as well as occasional and facultative cleaner. Main cleaner fish of every group comprise small species, young labrid specimens are mostly facultative ones. In some areas also gobiids and chaetodontids are active cleaner. Many cleaner species present a unique, conspicuous coloration, especially in tropic areas, whereas in several temperate climate areas the cleaner fish present other color markings which are recognized by the clients. In the Indo-Westpacific some fang blennies like *Aspidontus taeniatus* (parasite), *Aspidontus. dussumieri* (herbivorous!) and *Plagiotremus tapeinosoma* (parasite) may be either imitator or model of cleaner wrasse coloration. These species create together with *Labroides dimidiatus* a mimicry ring including Bates', Mueller's and Peckham's mimicry (Zander 2017). A similar phenomenon was found in the Mediterranean basing on the young facultative cleaner *Coris julis* (fig. 1d; Zander & Nieder 1999). An additional possible characteristic by which cleaner fish may be identified is the seesawing mode of swimming and accentuated by special dancing movements which is displayed by labrids and imitated by fang blennies (Wickler 1968).

An argument for an origin of cleaning behavior from commensalism is the greater abundance of e.g. *L. dimidiatus* than of the parasite *A. taeniatus* (Zander 2017). The basis for this assumption may be a narrow body contact as occurs in feeding partnerships and was observed in Mediterranean labrids (Zander et al. 1999). It is generally known that cleaner fish remove also ulcer from the skin of clients. Another evidence for an origin from commensalism was revealed by prey analyses of the Mediterranean main cleaner, *Symphodus melanocercus*, which preferred parasites before skin from their clients or sometimes even plankton (fig. 2; Detloff et al. 2010). The mentioned situation of the Danube river regarding six fish species which are mutually cleaner and hosts may emphasize a first level of this symbiosis (Abel 1971).

Some authors, however, argument that the cleaner symbiosis might have derived from parasitism (Grutter & Bschary 2003). They found that fish skin is a more attractive prey than parasites. Mucus as prey of cleaner fish is worldwide distributed either as additional prey as was observed in the Mediterranean *S. melanocercus* and the Indo-Pacific *L. dimidiatus* (Grutter & Bschary 2003) or exclusively as shown by the Hawaiian *Labroides phthiriphagus* (Gorlick 1980; Losey 1999). Among fang blennies of which several species have evolved onto parasitism no cleaner is known. If cleaner fish act as occasional parasites they feed the more on skin and mucus the lower the density of crustacean parasites is (Grutter 2005).

According to Grutter (2005) cleaning in labrids has evolved from feeding on epifauna. The drive may be the fitness benefits to both partners (Poulin &Vickery 1995). But Losey (1999) propagated that parasitism as shown by Hawaiian *Labroides* spp. has been the starting point of cleaning. Thus, during evolution very probably different paths may lead to this symbiosis. Contacts of labrids to other fish, mostly in feeding assemblages, occur very often (Moosleitner 1979, 2008; Zander 2016; Zander & Nieder 1999). Obviously, especially young stages of several species act as cleaners (Coté 2000). Cleaner must be of far smaller size than their clients in order to find parasites on skin and fins and also in the mouth and on the gills. Labrids are predisposed for this task by morphology of jaws and teeth and by their small size. The same may be valid for cleaning chaetodontids and pomacanthids, whereas *Echineis naucrates* is main cleaner of large clients. In

contrast, fang blennies are predisposed by their long canine teeth that have evolved rather for a parasitic mode of life, but not for a life as cleaners.

Therefore, it is to assume that cleaning symbiosis is a result of different evolutionary paths originating as well from commensalism as from parasitism.

Literature

Abel, E. F. 1971. Zur Ethologie von Putzsymbiosen einheimischer Süßwasserfische im natürlichen Biotop. Oecologia 6, 133-151.

Costello, M. 1991. Review of the biology of wrasse (Labridae: Pisces) in Northern Europe: Options and the use of cleaner fish. World Aquaculture 24, 40-56.

Coté, I. 2000. Evolution and ecology of cleaning symbioses in the Sea. Oceanography and Marine Biology: An Annual Review 38, 311-355.

de Bary, A. 1878. Die Erscheinung der Symbiose. Trübner, Strassburg.

Dethloff, K., Zander, C.D., Brisant, N., & D. Ziggel. 2010. Seasonal variation in the feeding activities of the facultative cleaner fish *Symphodus melanocercus* (Risso 1810) in the Tyrrhenian Sea (Italy). Bulletin of Fish Biology 12, 15-26.

Eibl.-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere zwischenartliche Beziehungen bei tropischen Meeresfischen. Zeitschrift für Tierpsychologie 12, 203-219.

Eibl.-Eibesfeldt, I. 1959. Der Fisch *Aspidontus taeniatus* als Nachahmer des Putzers *Labroides dimidiatus*. Zeitschrift für Tierpsychologie 16, 19-25.

Gorlick, D. L. 1980. Ingestion of host fish surface mucus by the Hawaiian USA cleaning wrasse, *Labroides phthirophagus*, Labridae, and its effect on host species preference. Copeia 1980, 863-868.

Grutter, A. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. Marine Ecology Progress Series 118, 51-58.

Grutter, A. 2005. Cleaning mutualism in the Sea, pp. 264-278. In: Marine Parasitology (Rohde, K., ed.). CSIRO Publishing, Collingwood VIC, Australia.

Grutter, A., & R. Bschary. 2003. Cleaner fish prefer client mucus: support for partner control mechanism in cleaning interactions. Proceedings of the Royal Society, Biological Sciences Series B, Biological Letters Supplement 2, S242-S244.

Losey, G.S., A. S. Grutter, G. Rosenquist, J. L. Mahon & J. P. Zamon. 1999. Cleaning symbiosis: a review, pp. 379-395. In: Behaviour and conservation of littoral fishes (Almada, V.C., R.F. Oliveira, & E.J. Gonçalves, eds). ISPA, Lisboa.

Margulis, L. 1970. Origin of eucariotic cells. Yale University Press, New Haven.

Merezhkowsky, C. 1905. Über Natur und Ursprung der Chromatophoren im Pflanzen-Reiche. Biologisches Centralblatt 15, 278-303, 321-347, 353-367.

Moosleitner, H. 1979. Feeding associations on sandy bottoms in the Mediterranean. Zoologischer Anzeiger 209, 269-282.

Moosleitner, H. 2008. Fressgemeinschaften mit Meerbarben (Mullidae) im tropischen Indo-Westpazifik. Bulletin of Fish Biology 10, 55-77.

Poulin, R., & L. W. Vickory. 1995. Cleaning symbiosis as an evolutionary game: to cheat or not to cheat. Journal of Theoretical Biology 175, 63-70.

Price, P. 1980. Evolutionary biology of parasites. Princeton University Press; Princeton.

Treasurer, J. 1993. Prey selection and daily food consumption by a cleaner fish, Ctenolabrus rupestris (L.) on farmed Atlantic salmon, Salmo salar L. Aquaculture 122, 269-277.

van Tassell, L., A. Brito, & A.S. Bortone. 1994. Cleaning behavior among marine fishes and invertebrates in the Canary Islands. Cybium 18, 117-127.

von Wahlert, G., & H. von Wahlert. 1971. Le comportement de nettoyage de *Crenilabrus melanocercus* (Labridae, Pisces) en Méditerranée. Vie et Milieu 12, 1-10.

Wallin, I.E. 1927. Symbionticism and the origin of species. Baillere, Tindall & Cox; London.

Wickler, W. 1968. Mimikry. Kindler; München.

Wirtz, P. 1995. Krebs-Seeanemonen-Symbiosen bei Madeira. Natur und Museum 125, 137-142.

Zander, C.D. 1917. The role of parasitic fish in pseudocave ecosystems of the Red Sea. Bulletin of Fish Biology 17, 53-57.

Zander, C.D., Meyer, U., & A. Schmidt. 1999. Cleaner fish symbiosis in European and Macaronesian waters, pp. 397-422. In: Behaviour and conservation of littoral fishes (Almada, V.C., R.F. Oliveira, & E. J. Gonçalves, eds). ISPA, Lisboa.

Zander, C.D., & J. Nieder. 1997. Interspecific associations in Mediterranean fishes: feeding communities, cleaning symbioses and cleaner mimics. Vie et Milieu 47, 203-212.

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Wallin 1927; Margulis 1970). In contrast, animal endoparasites live in body cavities of other metazoans, such as free living turbellarian platyhelminths that entered as commensals gill cavities of fish and crayfish hosts and are assumed to evolve by this way to endoparasitic groups of platyhelminths (Price 1980). Ectoparasitism may have developed from animals which use the hosts as vehicles in order to attain comfortable habitat changes. This was the way which many crustaceans have persuaded onto skin or fins of fish prior to become parasites (Costello 1991; Treasurer 1993).

Since the description by Eibl-Eibesfeldt (1955) the cleaner symbiosis was an outstanding example for mutualism. This author observed the gobiid *Gobiosoma* spp. in the Caribbean, which pick off parasitic crustaceans from skin and fins of other fish species. Most research on cleaner fish was done on the labrid *Labroides dimidiatus* from the Indo-Westpacific. The cleaner profits by getting prey, the host profits from the loss of blood sucking parasites. This view on cleaner mutualism had been changed when Gorlick (1980) detected that the gut of the cleaner fish *Labroides phthirophagus* from Hawaii was filled with more mucus of fish than with parasitic crustaceans.

Therefore, the following compilation of results regarding cleaner fish observations from different areas of the world may contribute to the question, whether the cleaning symbiosis may be derived from commensalism or parasitism. An important pattern is the so called international cleaner dress which is presented by *Echineis naucrates*: a blue stripe along a light body.

2. Methods

For the following text and table 1 cleaner and parasite fish are classified to self created categories:
main cleaner – species which dominate as cleaner,
facultative cleaner – species which support main cleaners, mostly young individuals,
occasional cleaner – species which feed on other organisms than parasites as main food,
main parasites – species which feed predominantly on mucus or scales of other fish,
occasional parasites – species which are cleaner but sometimes behave as parasites.

3. Results

3.1. Circumtropical distribution

Echineis naucrates (Echineidae) (fig. 1a) is found in oceans around the world. This species presents a coloration which is model and imitated by several other cleaner fish, e.g. by the labrid *Labroides dimidiatus* or by the gobiids *Gobiosoma oceanops* and *G. evelynae*, but also by the parasitic *Aspidontus taeniatus* (Blenniidae) (Eibl-Eibesfeldt 1959).

Fig. 1: Representatives of cleaner fish around the world. **a** *Echineis naucrates* (Echineidae) is distributed in all seas of the tropic regions. Its coloration may be the model for several other cleaner fish species. **b** *Ctenolabrus rupestris* (Labridae) is a facultative cleaner in the North-East Atlantic. The dark spot on the tail may be the signal to be recognized by clients. **c** *Symphodus melanocercus* (Labridae) (here persuading a *Chromis chromis*) is a main cleaner in the Mediterranean Sea; its black tail mark is acknowledged by clients. **d** Young *Coris julis* (Labridae) are facultative cleaners; their characteristic coloration is similar to *E. naucrates* but with a brown horizontal line instead of a dark blue one. **e** *Labroides dimidiatus* (Labridae) (here with its client *Scolopsis ghanam*) is the main cleaner in the Indo-West-Pacific and imitator of the characteristic cleaner coloration of *E. naucrates*. **f** Young *Larabicus quadrilineatus* (Labridae) are facultative cleaners in the Red Sea. The bright blue body coloration differs slightly from that of *E. naucrates* (Photo: R. Gramckow). **g** *Johnrandallia nigrirostris* (Chaetodontidae) is main cleaner in the Galapagos-Archipelago. **h** *Gobiosoma evelynae* (Gobiidae) is one of main cleaner fish in the Caribbean Sea, its coloration is in accordance with the characteristic cleaner uniform.
Abb. 1: Einige Repräsentanten der Putzerfisch-Gilde aus der ganzen Welt. **a** *Echineis naucrates* (Echineidae) kommt in allen tropischen Meeren vor. Seine Färbung ist das Vorbild für viele andere Putzerfisch-Arten. **b** *Ctenolabrus rupestris* (Labridae) ist fakultativer Putzer im Nord-Ost-Atlantik. Der schwarze Fleck an der

Schwanzwurzel mag das entscheidende Signal für potenzielle Kunden sein. **c** *Symphodus melanocercus* (Labridae) ist der Hauptputzer im Mittelmeer. An der schwarzen Schwanzmarkierung wird er von seinen Kunden erkannt. **d** Jungfische von *Coris julis* (Labridae) sind fakultative Putzer, seine Färbung ähnelt der von *E. naucrates*, allerdings ist das dunkle Längsband braun. **e** *Labroides dimidiatus* (Labridae) (hier mit *Scolopsis ghanam*) ist der Hauptputzer im Indo-Westpazifik und ahmt die Färbung von *E. naucrates* nach. **f** Jungfische von *Larabicus quadrilineatus* (Labridae) putzen fakultativ im Roten Meer. Die hellblaue Körperfärbung weicht geringfügig von der des Vorbilds *E. naucrates* ab (Foto: R. Gramcko). **g** *Johnrandallia nigrirostris* (Chaetodontidae) ist der Hauptputzer im Galapagos-Archipel. **h** *Gobiosoma evelynae* (Gobiidae) ist einer der Hauptputzer in der Karibik, seine Färbung gleicht der charakterischen Putzertracht von *E. naucrates*.

3.2. Northeast Atlantic, including North Sea

Here the labrid *Ctenolabrus rupestris* is a facultative cleaner, which is often used in salmon farms in order to free these fish from parasitic copepods (Costello 1991; Treasurer 1993). Its coloration is not remarkable with exception of a black spot on the tail (fig. 1b). Additionally, young of several larger *Labrus* and *Symphodus* spp. (Labridae) are occasional cleaners. No parasite fish feeding on mucus and skin of other fish are known from this region.

3.3. Mediterranean Sea

In this region the small labrid *Symphodus melanocercus* (fig. 1c) is the main cleaner (von Wahlert & von Wahlert 1961; Zander & Nieder 1997; Zander et al. 1999), supported by young of the labrids *Coris julis* (fig. 1d) and *Thalassoma pavo*. Young *C. julis* have similar colorations as *E. naucrates* except that the longitudinal stripes are brown, young *T. pavo* have dark brown patterns on the sides, whereas *S. melanocercus* is conspicuous by a black marking on the tail which functions as signal for clients. Juveniles of several other *Symphodus* spp. were observed to clean occasionally. Cardinal fish (*Apogon imberbis*) are exclusively cleaned by young *Coris julis*, morays (*Muraena helena*), however, only by shrimps. Exclusive parasitic behavior of any fish species was not observed in this region. Evidently, *S. melanocercus* feeds on benthos, sometimes on plankton and is an occasional parasite (fig. 2, Detloff et al. 2010).

3.4. Subtropical East-Atlantic (Acores, Madeira, Canaries)

Surprisingly, in this region no main cleaner fish is present. Facultative cleaners are the young of the labrids *T. pavo* and *C. julis* such as in the Mediterranean. Also shrimps have a greater importance as cleaners than fish in this region (van Tassell et al. 1994; Wirtz 1995). In eastern Atlantic archipelagos no parasitic fish was observed until now.

3.5. Red Sea and West-Indopacific

In this wide area the labrid *Labroides dimidiatus* (fig. 1e) dominates as cleaner (Eibl-Eibesfeldt 1959). It imitates the worldwide cleaner coloration as do the facultative cleaner *L. bicolor* and *Thalassoma amblycephalus*. Young *Larabicus quadrilineatus,* which are endemic and facultative cleaner in the Red Sea, differ somewhat by coloration in that the body is bluish (fig. 1f). Unexpectedly, young individuals of the chaetodontid *Heniochus acuminatus* are facultative cleaners. In this region the parasite fang blenny *A. taeniatus*, whose coloration resembles that of *L. dimidiatus* (Eibl-Eibesfeldt 1959), is abundant. This camouflage confuses potential hosts of cleaners so that the parasite can approach the client and prey on pieces of skin and fins. The fang blenny *Plagiotremus rhinorhynchus* behaves in a similar way but its coloration differs by its broken blue line from the model (Zander 2017). On the other side, Grutter (1996) observed that *L. dimidiatus* feeds in the

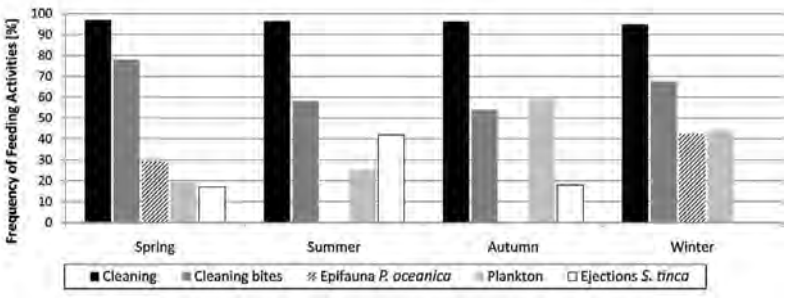

Fig. 2: Frequency of seasonal feeding activities of *Symphodus melanocercus* (from Detloff et al. 2010).
Abb. 2: Fressaktivität (Frequenzen) von *Symphodus melanocercus* im Jahresverlauf (aus Detloff et al. 2010).

Great Barrier Reef not only on parasites but also on skin from their clients therefore, it is an occasional parasite.

3.6. East Pacific (Galapagos, Hawaii)

Surprisingly, in Galapagos main cleaner is neither a labrid nor a gobiid. Main cleaners are beside *E. naucrates* (cleans large clients) the chaetodontid *Johnrandallia nigrirostris* (fig. 1g). Young of the labrids *Bodianus diplotaenia* and *Thalassoma lucasanum* as well as adults of the small-sized gobiid *Gobiosoma digueti* clean occasionally. In Hawaii prevails a special situation, because the endemic *Labroides phthiriphagus* is more parasite than occasional cleaner (Gorlick 1980). Other parasites are several *Plagiotremus* spp., but occasional cleaner in Hawaii are adult and young *Thalassoma duperrey*.

3.7. Caribbean

Main cleaners are the gobiids *Gobiosoma evelynae* (fig. 1h) and *Gobiosoma oceanops*, which present the characteristic cleaner coloration of *E. naucrates* and *L. dimidiatus*. In this area the cleaner symbiosis was at first at all observed by Eibl-Eibesfeldt (1955). Several young labrids like *Thalassoma bifasciatum* or young pomacanthids like *Paracanthus paru* are facultative cleaners.

3.8. Freshwater Europe

Only few occasional observations are known from fresh waters In the River Danube, Abel (1971) observed that *Scardinius erythrophthalmus* has a central position, because it cleans *Alburnus alburnus*, *Tinca tinca, Rutilus rutilus* and conspecifics, but is cleaned itself by *A. alburnus* and

Tab. 1: Compilation of known cleaners and parasitic fish in diverse regions of the world. Compiled according to the cited literature.
Tab. 1: Zusammenstellung bekannter Putzer und parasitischer Fische aus verschiedenen Regionen der Welt. Zusammengestellt nach der genannten Literatur.

	Main cleaner	Facultative cleaner	Occasional cleaner	Parasites	Occasional parasites
Nordeast-Atlantik/North Sea		*Ctenolabrus rupestris*	*Labrus* spp. juv *Symphodus* spp. juv.		
Mediterranean Sea	*Symphodus melanocercus*	*Coris julis* juv. *Thalassoma pavo* juv.	*Symphodus* spp. juv		*Symphodus melanocercus*
Subtropical East-Atlantik Acores, Madeira, Canary archipelagos		*Thalassoma pavo* juv. *Coris julis* juv.			
Tropical East-Atlantik Cap Verde	*Echineis naucrates*	*Thalassoma pavo* juv. *Holocanthus africanus* juv.			
Red Sea, Indo-Westpazifik	*Echineis naucrates* *Labroides dimidiatus*	*Labroides bicolor* *Larabicus quadrilineatus* juv. *Thalassoma amblycephalus* juv. *Heniochus acuminatus juv.*		*Aspidontus taeniatus* *Plagiotremus rhinorhynchus*	*Labroides dimidiatus*
Eastpazific Galapagos, Hawaii	*Echineis naucrates* *Johnrandallia nigrirostris*	*Gobiosoma digueti* *Bodianus diplotenia juv.* *Thalassoma lucasanum juv.*	*Labroides phthiriphagus*	*Labroides phthiriphagus* *Plagiotremus azalea* P. ewaensis *P. gosline*	
Caribbean Sea	*Echineis naucrates* *Gobiosoma evelynae* *Gobiosoma oceanops*	*Thalassoma bifasciatus juv.* *Pomacnthus paru juv.*			
Fresh water Europe Danube River		*Rhodeus amarus* *Scardinius erythrophthalmus* *Alburnus alburnus* *Rutilus rutilus* *Tinca tinca*	*Perca fluviatilus* juv.		

Rhodeus sericeus. *R. rutilus* probably cleans *Perca fluviatilis* that cleans also conspecifics. Intraspecific cleaning is generally characteristic within this fish assemblage.

4. Discussion

The most noteworthy results of the present article are: 1) the coloration of cleaner fish is a signal for their clients. 2) Changes from a cleaning to a parasitic way of life are flowing; several facts give evidence for an origin of cleaning symbioses from commensalism as well as from parasitism

At most, labrids take over the role as main cleaner as well as occasional and facultative cleaner. Main cleaner fish of every group comprise small species, young labrid specimens are mostly facultative ones. In some areas also gobiids and chaetodontids are active cleaner. Many cleaner species present a unique, conspicuous coloration, especially in tropic areas, whereas in several temperate climate areas the cleaner fish present other color markings which are recognized by the clients. In the Indo-Westpacific some fang blennies like *Aspidontus taeniatus* (parasite), *Aspidontus. dussumieri* (herbivorous!) and *Plagiotremus tapeinosoma* (parasite) may be either imitator or model of cleaner wrasse coloration. These species create together with *Labroides dimidiatus* a mimicry ring including Bates', Mueller's and Peckham's mimicry (Zander 2017). A similar phenomenon was found in the Mediterranean basing on the young facultative cleaner *Coris julis* (fig. 1d; Zander & Nieder 1999). An additional possible characteristic by which cleaner fish may be identified is the seesawing mode of swimming and accentuated by special dancing movements which is displayed by labrids and imitated by fang blennies (Wickler 1968).

An argument for an origin of cleaning behavior from commensalism is the greater abundance of e.g. *L. dimidiatus* than of the parasite *A. taeniatus* (Zander 2017). The basis for this assumption may be a narrow body contact as occurs in feeding partnerships and was observed in Mediterranean labrids (Zander et al. 1999). It is generally known that cleaner fish remove also ulcer from the skin of clients. Another evidence for an origin from commensalism was revealed by prey analyses of the Mediterranean main cleaner, *Symphodus melanocercus*, which preferred parasites before skin from their clients or sometimes even plankton (fig. 2; Detloff et al. 2010). The mentioned situation of the Danube river regarding six fish species which are mutually cleaner and hosts may emphasize a first level of this symbiosis (Abel 1971).

Some authors, however, argument that the cleaner symbiosis might have derived from parasitism (Grutter & Bschary 2003). They found that fish skin is a more attractive prey than parasites. Mucus as prey of cleaner fish is worldwide distributed either as additional prey as was observed in the Mediterranean *S. melanocercus* and the Indo-Pacific *L. dimidiatus* (Grutter & Bschary 2003) or exclusively as shown by the Hawaiian *Labroides phthiriphagus* (Gorlick 1980; Losey 1999). Among fang blennies of which several species have evolved onto parasitism no cleaner is known. If cleaner fish act as occasional parasites they feed the more on skin and mucus the lower the density of crustacean parasites is (Grutter 2005).

According to Grutter (2005) cleaning in labrids has evolved from feeding on epifauna. The drive may be the fitness benefits to both partners (Poulin &Vickery 1995). But Losey (1999) propagated that parasitism as shown by Hawaiian *Labroides* spp. has been the starting point of cleaning. Thus, during evolution very probably different paths may lead to this symbiosis. Contacts of labrids to other fish, mostly in feeding assemblages, occur very often (Moosleitner 1979, 2008; Zander 2016; Zander & Nieder 1999). Obviously, especially young stages of several species act as cleaners (Coté 2000). Cleaner must be of far smaller size than their clients in order to find parasites on skin and fins and also in the mouth and on the gills. Labrids are predisposed for this task by morphology of jaws and teeth and by their small size. The same may be valid for cleaning chaetodontids and pomacanthids, whereas *Echineis naucrates* is main cleaner of large clients. In

contrast, fang blennies are predisposed by their long canine teeth that have evolved rather for a parasitic mode of life, but not for a life as cleaners.

Therefore, it is to assume that cleaning symbiosis is a result of different evolutionary paths originating as well from commensalism as from parasitism.

Literature

Abel, E. F. 1971. Zur Ethologie von Putzsymbiosen einheimischer Süßwasserfische im natürlichen Biotop. Oecologia 6, 133-151.

Costello, M. 1991. Review of the biology of wrasse (Labridae: Pisces) in Northern Europe: Options and the use of cleaner fish. World Aquaculture 24, 40-56.

Coté, I. 2000. Evolution and ecology of cleaning symbioses in the Sea. Oceanography and Marine Biology: An Annual Review 38, 311-355.

de Bary, A. 1878. Die Erscheinung der Symbiose. Trübner, Strassburg.

Dethloff, K., Zander, C.D., Brisant, N., & D. Ziggel. 2010. Seasonal variation in the feeding activities of the facultative cleaner fish *Symphodus melanocercus* (Risso 1810) in the Tyrrhenian Sea (Italy). Bulletin of Fish Biology 12, 15-26.

Eibl.-Eibesfeldt, I. 1955. Über Symbiosen, Parasitismus und andere zwischenartliche Beziehungen bei tropischen Meeresfischen. Zeitschrift für Tierpsychologie 12, 203-219.

Eibl.-Eibesfeldt, I. 1959. Der Fisch *Aspidontus taeniatus* als Nachahmer des Putzers *Labroides dimidiatus*. Zeitschrift für Tierpsychologie 16, 19-25.

Gorlick, D. L. 1980. Ingestion of host fish surface mucus by the Hawaiian USA cleaning wrasse, *Labroides phthirophagus*, Labridae, and its effect on host species preference. Copeia 1980, 863-868.

Grutter, A. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. Marine Ecology Progress Series 118, 51-58.

Grutter, A. 2005. Cleaning mutualism in the Sea, pp. 264-278. In: Marine Parasitology (Rohde, K., ed.). CSIRO Publishing, Collingwood VIC, Australia.

Grutter, A., & R. Bschary. 2003. Cleaner fish prefer client mucus: support for partner control mechanism in cleaning interactions. Proceedings of the Royal Society, Biological Sciences Series B, Biological Letters Supplement 2, S242-S244.

Losey, G.S., A. S. Grutter, G. Rosenquist, J. L. Mahon & J. P. Zamon. 1999. Cleaning symbiosis: a review, pp. 379-395. In: Behaviour and conservation of littoral fishes (Almada, V.C., R.F. Oliveira, & E.J. Gonçalves, eds). ISPA, Lisboa.

Margulis, L. 1970. Origin of eucariotic cells. Yale University Press, New Haven.

Merezhkowsky, C. 1905. Über Natur und Ursprung der Chromatophoren im Pflanzen-Reiche. Biologisches Centralblatt 15, 278-303, 321-347, 353-367.

Moosleitner, H. 1979. Feeding associations on sandy bottoms in the Mediterranean. Zoologischer Anzeiger 209, 269-282.

Moosleitner, H. 2008. Fressgemeinschaften mit Meerbarben (Mullidae) im tropischen Indo-Westpazifik. Bulletin of Fish Biology 10, 55-77.

Poulin, R., & L. W. Vickory. 1995. Cleaning symbiosis as an evolutionary game: to cheat or not to cheat. Journal of Theoretical Biology 175, 63-70.

Price, P. 1980. Evolutionary biology of parasites. Princeton University Press; Princeton.

Treasurer, J. 1993. Prey selection and daily food consumption by a cleaner fish, Ctenolabrus rupestris (L.) on farmed Atlantic salmon, Salmo salar L. Aquaculture 122, 269-277.

van Tassell, L., A. Brito, & A.S. Bortone. 1994. Cleaning behavior among marine fishes and invertebrates in the Canary Islands. Cybium 18, 117-127.

von Wahlert, G., & H. von Wahlert. 1971. Le comportement de nettoyage de *Crenilabrus melanocercus* (Labridae, Pisces) en Méditerranée. Vie et Milieu 12, 1-10.

Wallin, I.E. 1927. Symbionticism and the origin of species. Baillere, Tindall & Cox; London.

Wickler, W. 1968. Mimikry. Kindler; München.

Wirtz, P. 1995. Krebs-Seeanemonen-Symbiosen bei Madeira. Natur und Museum 125, 137-142.

Zander, C.D. 1917. The role of parasitic fish in pseudocave ecosystems of the Red Sea. Bulletin of Fish Biology 17, 53-57.

Zander, C.D., Meyer, U., & A. Schmidt. 1999. Cleaner fish symbiosis in European and Macaronesian waters, pp. 397-422. In: Behaviour and conservation of littoral fishes (Almada, V.C., R.F. Oliveira, & E. J. Gonçalves, eds). ISPA, Lisboa.

Zander, C.D., & J. Nieder. 1997. Interspecific associations in Mediterranean fishes: feeding communities, cleaning symbioses and cleaner mimics. Vie et Milieu 47, 203-212.

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