Population Demographics and Life History Characteristics of *Heliofungia actiniformis*:

A Fungiid Coral Species Exploited for the Live Coral Aquarium Trade in the Spermonde Archipelago, Indonesia

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Für meine Großmutter…

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zmt bremen

UFT Zentrum für Umweltforschung und Umwelttechnologie

CENTER FOR CORAL REEF RESEARCH HASANUDDIN UNIVERSITY

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Summary

The international aquarium industry currently trades an estimated 11-12 million pieces of live scleractinian corals a year, of which over 90% originate from Indonesia. In order to ensure harvest sustainability as well as the compliance with CITES requirements, the Indonesian government is at present applying a number of management strategies. These include licensing requirements for companies and fishermen, the setting of quotas, the prohibition of coral collection in marine protected areas and attempts at creating viable ecolabelling schemes. The trade is however dominated by colourful large polyped coral species, for which very little biological data is available. Moreover, scientific knowledge about the population dynamics of scleractinian coral species in general is very limited, and present management plans are as a result based on little more than arbitrary decisions. The general aim of this thesis was to address this poor scientific foundation of management regimes. In order to achieve this, a multi-disciplinary case-study approach, which focussed on one of the most important species in the Indonesian aquarium trade, the mushroom coral *Heliofungia actiniformis*, was used.

In chapter two, the results of an investigation into the population dynamics of *H. actiniformis* at three unharvested sites are presented. Growth rates decreased linearly with increasing polyp length, from 1.2 cm yr^{-1} for the youngest polyps to 0.1 cm yr^{-1} for the oldest polyps. Relative to other mushroom corals *H. actiniformis* reached reproductive maturity and maximum biomass production at the late ages of 10 and 20 years respectively, rendering the species especially vulnerable to overexploitation. The population size / age structure was dominated by young attached polyps budding from clusters of stalks attached to the reef, with each cluster originating from the settlement of a sexually produced larva. The great majority of corals detached from stalks before attaining 4 cm in length, reaching the free living life history phase typical of mushroom corals. Although stalks capable of reproducing tentacles and eventually polyps have been noted for other species in the past, such proliferal asexual reproduction by reef stalks seems unique to *H. actiniformis*, and was described in detail for the first time by the present investigation. Neither the settlement of sexual recruits nor their asexual budding showed seasonality, so that it a single population census, albeit but a snapshot in time, gave an accurate representation of population structure during the study period.

The attached polyps suffered high natural mortality rates in comparison to those of the free-living individuals, which were an order of magnitude lower. Although there were no

statistically significant differences in the overall mortality rates or the age-frequency distributions of polyps aged 0-15 years between sites, differences in the abundance of large *H. actiniformis* polyps at the three replicate sites were found, and could be correlated with variations in rubble cover. The site with the lowest amount of coral rubble had a higher number of polyps aged 40 years and above, which are likely to have suffered higher mortality rates due to storm rubble avalanches at the two sites with less stable habitat substratum. Young detached polyps are able to inflate body tissue and overturn after such substratum shifts, potentially rendering them less vulnerable.

In chapter three details on levels of genetic population connectivity revealed by research on the genetic structure of *H. actiniformis* corals throughout the Indo-Malay Archipelago are discussed. Significant genetic structuring was found at both the small scale, among populations in the Spermonde Archipelago, and at the large scale, throughout the Indo-Malay Archipelago. At both scales the degree of geographic separation as well as local oceanographic features influenced the level of genetic structuring, with nearby populations and those connected by currents having a higher degree of larval exchange and thus less differences in the genetic make-up of organisms. Overall the data indicated that although the brooded and thus well developed larvae of *H. actiniformis* frequently settle on nearby reefs, maintaining genetic structures on the small scale, a significant proportion is also dispersed more widely by current entrainment. The imprint of historical influences was however also found in *H. actiniformis* populations on the Sahul shelf, which were significantly different from populations in the nearby Flores Sea despite the presence of local connecting currents. Despite the confounding influences of historical factors on present day population genetic structuring, several management implications arise from the patterns uncovered by the present study. In particular the collection of organisms in upstream as well as more isolated sites should be treated with caution, since the potential for larval input from surrounding populations is less likely here, and thus populations are more vulnerable to overexploitation.

In Chapter four, the focus is on the impacts of the marine ornamental trade on *H. actiniformis* populations in the Spermonde Archipelago, one of four major coral collection sites in the Indonesian Archipelago. Semi-structured interview surveys with coral collectors revealed a size-selective fishery towards small polyps, driven by a demand for corals that are easy to fit into home aquaria and transport from collection sites to consumers. *In situ* surveys at harvested sites revealed a shift in size-frequency distributions as well as reduced overall abundances in comparison to unharvested sites. Fishing mortality rates significantly exceeded natural mortalities known from previous investigations for polyps aged 0-11 years, with exploitation rates of 0.1 and 0.7 for polyps sized 0-4 cm, and 4-11 cm respectively.

In order to provide potential future management approaches based on sound scientific advice, finfish stock assessment models were for the first time tested as tools for the evaluation of live coral harvesting regimes. The Beverton and Holt biomass yield per recruit model was tested in combination with a utility per recruit approach. This revealed that maximum potential economic yield in fact occurred at a size of 5 cm and a corresponding age of 5 years, 15 years before the attainment of maximum biomass yield per recruit. Since the demand is for small corals in this species, and fragmentation of large individuals not an option as in some other exploited species, gearing harvesting strategies at obtaining maximum biomass yield per recruit is not feasible.

This market demand for young polyps however also means that reproductively immature polyps are targeted by the fishery: *H. actiniformis* only reaches reproductive maturity at a size of ~9 cm. Achieving long term sustainability will thus necessitate an effective protection of spawning stocks, ideally through a combination of quota restrictions and marine protected areas. Indeed, the present exploitation rate of 0.7 is too high, and only a limited number of large polyps was found at harvested sites. Remarkably, the application of a Thompson and Bell predictive model indicated that in combination with a 5 cm size limit reducing harvest quotas and thus exploitation rates for polyps would in fact be possible without lowering current profits.

Overall the present study provides much needed data on the population dynamics of a coral species very popular in the marine ornamental trade. The fact that results revealed *H. actiniformis* to be very vulnerable to overexploitation, and at the same time indicated potentially simple yet effective management strategies, highlight the urgent need for similar studies. In particular research on coral larval connectivity patterns and a more general application of stock assessment models to management approaches of the live coral aquarium trade should be encouraged.

Zusammenfassung

Der internationale Aquarienhandel vertreibt derzeit jährlich eine geschätzte Menge von 11-12 Millionen Steinkorallenfragmenten, von denen über 90% aus Indonesien stammen. Um sowohl eine nachhaltige Korallenfischerei als auch die Einhaltung der CITES Richtlinien zu gewährleisten, unterliegt der Handel mit Korallen in Indonesien zur Zeit einigen von der Regierung festgesetzten Managmentrichtlinien. Diese beinhalten die Lizensierung von Händlern und Fischern, die Festlegung von Fangquoten, ein Verbot der Korallenentnahme in marinen Schutzgebieten und erste Versuche, ein Öko-Label einzuführen. Dies ist nur schwer umzusetzen, da der Korallenhandel von farbenprächtigen, großpolypigen Korallenarten dominiert wird, deren Biologie nur unzureichend erforscht ist. Hinzu kommt, dass generell nur wenig über die Populationsdynamik von Steinkorallen bekannt ist, so dass die derzeitigen Managementstrategien wissenschaftlich nicht fundiert sind. Das Ziel dieser Arbeit war es daher, durch eine interdisziplinäre Fallstudie eine wissenschaftliche Basis für zukünftige Managementpläne zu liefern. In diesem Zusammenhang wurde die Pilzkoralle *Heliofungia actiniformi*s, eine der wichtigsten Arten des indonesischen Handels mit Steinkorallen, untersucht.

In Kapitel zwei sind die Ergebnisse der populationsdynamischen Untersuchung von *H. actiniformis* an drei, nicht von der Fischerei beeinträchtigten Standorten, dargestellt. Die Wachstumsraten nahmen linear mit zunehmender Polypenlänge ab. Die jüngsten Korallen wuchsen 1,2 cm Jahr^{-1}, die ältesten hingegen nur 0,1 cm Jahr^{-1}. Im Vergleich zu anderen Pilzkorallenarten ist *H. actiniformis* besonders anfällig für Überfischung, da sie ihre Fortpflanzungsfähigkeit bzw. die maximale Biomasseproduktion erst in einem späten Alter von 10 bzw. 20 Jahren erreicht. Die Größen/Altersstruktur der Population zeigte eine Dominanz von jungen, noch am Riff festgewachsenen Polypen, wobei jedes Anthocaulus-Cluster aus einer einzigen sexuell entstandenen Larve hervorgegangen ist. Die überwiegende Mehrheit der Korallen löste sich von ihrem Anthocaulus, bevor sie eine Länge von 4 cm erreichten. An diese Phase schloss sich das für Pilzkorallen charakteristische freilebende Entwicklungsstadium an. Für andere Pilzkorallenarten wurde bereits das Phänomen beschrieben, dass sich aus den Anthocauli Tentakel und letztendlich neue Polypen bilden können. Wie diese Studie zum ersten Mal im Detail beschreibt, ist dieser Weg der asexuellen Reproduktion bei *H. actiniformis* besonders ausgeprägt. Weder die Ansiedlung der sexuellen Larven noch die asexuelle Knospung von Polypen zeigte eine saisonale Abhängigkeit.

Deswegen kann davon ausgegangen werden, dass während des Untersuchungszeitraums eine einmalige Erhebung ein korrektes Bild der Populationsstruktur ergab.

Die noch am Riff festgewachsenen Polypen erfuhren, verglichen mit frei lebenden Individuen, eine ungleich höhere natürliche Sterblichkeitsrate. Auch wenn keine statistisch signifikanten Unterschiede in den Gesamtmortatlitätsraten sowie der Häufigkeitsverteilung des Alters der 0-15 jährigen Polypen festgestellt werden konnten, unterschieden sich die drei Standorte in der Abundanz der großen *H. actiniformis* Individuen. Diese Unterschiede korrelierten mit den Variationen im Geröllanteil des Substrats. Dabei wies der Standort mit dem geringsten Geröllanteil eine höhere Anzahl von Polypen mit einem berechneten Alter von 40 Jahren und mehr auf. Junge freilebende Polypen können sich durch das Ausdehnen von Körpergewebe wieder in ihre ursprüngliche Position bringen, wenn sie, zum Beispiel nach einer Geröllawine umgedreht wurden. Dies ist bei größeren Polypen mit einem höheren Gewicht wahrscheinlich nicht möglich, was dazu führt, dass diese Größenklasse an Standorten mit viel Geröll höhere Mortalitätsraten aufweist.

In Kapitel drei werden Muster genetischer Konnektivität der *H. actiniformis* Populationen im indo-malayischen Archipel diskutiert, welche sich aus Untersuchungen der genetischen Populationsstruktur ergab. Eine signifikante Populationsstruktur wurde sowohl auf kleiner, d.h. zwischen Populationen innerhalb des Spermonde Archipels, als auch auf großer Skala, d.h. innerhalb des indo-malayischen Archipels, gefunden. Auf beiden Skalen spielten die geographische Entfernung wie auch lokale ozeanographische Gegebenheiten eine bedeutende Rolle. So waren nah gelegene Populationen und solche, die durch starke Strömungen verbunden waren, durch einen höheren Genfluß ausgezeichnet. Insgesamt zeigten die Daten zum einen, dass sich die weit entwickelten Larven von *H. actiniformis* bevorzugt auf nah gelegenen Riffen ansiedeln und sich somit auf kleinem Maßstab eine genetische Struktur entwickelt. Zum anderen wurde jedoch ein deutlicher Anteil an Larven durch Strömungen sehr viel weiter verbreitet. Die Populationen von *H. actiniformis* auf dem Sahul-Schelf trugen allerdings Spuren von historischen Einflüssen. Obwohl dieses Gebiet durch lokale Strömungen mit der angrenzenden Flores-See verbunden ist, unterschieden sich die Populationen signifikant voneinander. Dennoch impliziert das Muster der Konnektivität zwischen *H. actiniformis* Populationen potentielle Managementstrategien. Besondere Vorsicht ist bei der Korallenfischerei an stromaufwärts sowie isoliert gelegenen Standorten geboten, da hier die potentielle Larvenzufuhr von umgebenden Populationen geringer ist, was diese Gebiete besonders anfällig für Überfischung macht.

In Kapitel vier liegt der Schwerpunkt auf den Einflüssen der Korallenentnahme auf Populationen von *H. actiniformis* im Spermonde Archipel, einem von vier Hauptstandorten für den marinen Aquarienhandel in Indonesien. Umfragen mit Fischern ergaben eine größenselektive Entnahme, die kleine Polypen bevorzugt. Dieses ergibt sich aus einer großen Nachfrage an Korallen, die in das heimische Aquarium passen und problemlos vom Ursprungsort bis zum Verbraucher zu transportieren sind. *In situ* Untersuchungen der befischten Standorte zeigten eine Verlagerung der Größenstruktur der Population sowie eine reduzierte Abundanz verglichen mit unbefischten Gebieten. Es konnte festgestellt werden, dass die Mortalitätsraten durch die Fischerei signifikant größer waren als die natürlichen Mortalitätsraten für Polypen in der Altersklasse 0-11 Jahre, wobei die Ausbeutungsraten für 0,1 für 0-4 cm, bzw. 0,7 für 4-11 cm große Polypen betrugen.

Modelle zur Bestimmung von Fischbeständen wurden erstmalig als Hilfsmittel zur Evaluierung des Korallenfischereiregimes angewendet, um eine wissenschaftlich fundierte Basis für die Entwicklung von zukünftigen Managementstrategien zu liefern. Das Beverton-Holt Ertrag/Rekrut-Modell wurde in Kombination mit einem Nutzen/Rekrut-Modell angewandt. Dies ergab einen maximalen potentiellen ökonomischen Wert, wenn *H. actiniformis*-Polypen in einer Größe von 5 cm, entsprechend einem Alter von 5 Jahren, gefischt werden. Dieser Zeitpunkt liegt 15 Jahre vor dem Erreichen des maximalen Biomasseertrags pro Individuum. Da jedoch die Nachfrage an dieser Koralle sich auf kleine Polypen beschränkt und eine Fragmentierung von großen Individuen bei dieser Art nicht möglich ist, kann man eine an dem Ertrag/Rekrut-Modell orientierte Managementstrategie nicht umsetzen.

Die Nachfrage nach kleinen Polypen von *H. actiniformis* bedeutet allerdings, dass die Organismen ihre sexuelle Fortpflanzungsfähigkeit bei Entnahme noch nicht erreicht haben. Um eine langfristige Nachhaltigkeit zu gewährleisten, ist der Schutz des Laichbestandes unbedingt notwendig, idealerweise durch eine Kombination von reduzierten Sammelquoten und marinen Schutzgebieten. Die derzeitige Ausbeutungsrate von 0,7 ist in der Tat zu hoch, was sich in der Tatsache widerspiegelt, dass nur wenige große Polypen in befischten Gebieten gefunden werden konnten. Bemerkenswerterweise ließ die Anwendung des Thompson-Bell-Modells erkennen, dass eine Umsetzung von reduzierten Fangquoten in Kombination mit einer Größenbegrenzung von 5 cm keine Profiteinbußen zur Folge hätte.

Insgesamt liefert diese Arbeit wichtige grundlegende Daten über die Populationsdynamik einer im Aquarienhandel sehr beliebten Korallenart. Die Ergebnisse zeigten zum einen, dass *H. actiniformis* sehr anfällig ist für Überfischung, und zum anderen, dass mit einfachen

Managementstrategien eine effektive Wirkung erzielt werden kann. Dies unterstreicht die Dringlichkeit der Durchführung ähnlicher Studien an weiteren Korallenarten. Insbesondere Untersuchungen der Konnektivität von Korallenpopulationen und die Anwendung von Ertragsmodellen sollten verstärkt eingesetzt werden, um nachhaltige Managementstrategien im Aquarienhandel zu erzielen.

List of Papers

This thesis is based on the scientific publications listed below. The specific contributions of each of the authors in terms of idea and concept development, data acquisition and analysis, as well as manuscript writing for the respective publications are indicated. Formatting in Chapters 2-4 was kept according to formatting requirements of the scientific journals the articles have been submitted to / are being published by, which are also specified.

Publication I

Title: Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia

Authors: L. Knittweis, M. Wolff, J. Jompa, C. Richter
Journal: Coral Reefs (submitted)

The original idea and concept of this publication was developed by L. Knittweis, who also independently conducted all of the fieldwork and sample processing. Data analysis was carried out by L. Knittweis, with input by M. Wolff. The publication manuscript was written by L. Knittweis, with revisions and improvements by M. Wolff, and C. Richter.

Publication II

Title: Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts.

Authors: L. Knittweis, W.E. Krämer, J. Timm, M. Kochzius
Journal: Conservation Genetics (in press, doi: 10.1007/s10592-008-9566-5)

The original idea and concept of this publication was developed by L. Knittweis and M. Kochzius. The great majority of samples was collected by L. Knittweis, with smaller contributions by J. Timm and M. Kochzius. Sample processing and data analysis was conducted by W. Krämer and L. Knittweis, with input from J. Timm and M. Kochzius. The publication manuscript was written by L. Knittweis, with revisions and improvements from the co-authors.

Publication III

Title: Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: potential future management approaches.

Authors: L. Knittweis, M. Wolff
Journal: Fisheries Research (submitted)

The original idea and concept of this publication was developed by L. Knittweis, who also independently conducted all of the fieldwork and sample processing. Data analysis was carried out by L. Knittweis, with input by M. Wolff. The publication manuscript was written by L. Knittweis, with revisions and improvements by M. Wolff.

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Chapter 1

Thesis Overview

Live coral for export, Spermonde, South Sulawesi

General introduction

The live coral aquarium trade

Around 2 million hobbyists keep marine aquaria around the world, and the global trade in marine ornamental species, which supplies these consumers with fish, corals and other invertebrates, is worth about US$ 200-330 million annually (Wabnitz et al. 2003). An estimated total of 140 scleractinian coral species are harvested and sold for the global aquarium trade, with a trade volume of 11-12 million pieces per year (Wabnitz et al. 2003). Dead corals, mainly the skeletons of genera with predominantly branching growth forms, accounted for more than 90% of the trade up to the early 1990s, but since then the quantity of live corals traded has increased tenfold. Unlike freshwater aquaria species, where most organisms traded are reared in captivity, over 99% of coral species for sale are collected from the wild (Green and Shirley 1999, Fig. 1). Colourful genera, often with large polyps, now dominate the trade, and despite the limitations of current trade data due to the difficulties in accurate coral identification, it is clear that species of *Trachyphyllia* spp., *Euphyllia* spp., *Goniopora* spp., *Acropora* spp., *Plerogyra* spp., *Catalaphyllia* sp., *Favia* spp., *Lobophyllia* spp., *Porites* spp., *Turbinaria* spp., *Montipora* spp. and *Heliofungia* sp. are the most popular (Wabnitz et al. 2003; Jones 2008). In addition 61 species of soft corals are also traded, in particular *Sarcophyton* spp. and *Dendronephthya* spp.

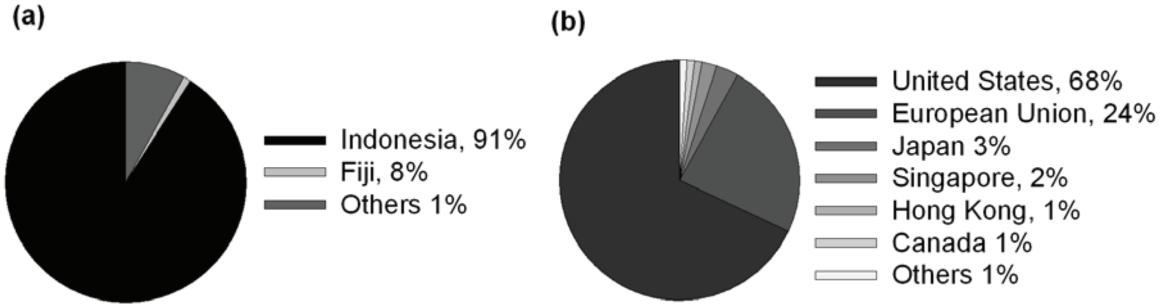


Fig. 1 (a) Exporters, (b) Importers of coral in 2005 as a percentage of the total (adapted from Jones 2008).

According to the CITES trade database, the top coral exporting countries in 2005 were Indonesia, Fiji, the Bahamas, the Solomon Islands and Tonga, with Indonesia playing by far the most important role: 91% of corals originate here (Fig. 1). This in fact represents an increase in 20% when compared to data from 2001, when only 71% of corals in the aquarium trade came from Indonesia (Jones 2008). The major importers of live ornamental coral in 2005 were the United States and the European Union, and to a lesser extent Japan, Singapore, Canada and Hong Kong (Fig. 1).

Impacts of coral harvesting

Hardly any of the species involved are exploited for other purposes, and aquarium animals are the highest value-added product that may be harvested from a coral reef (Wabnitz et al. 2003). It follows that if kept at sustainable levels, the industry could provide a valuable alternative source of income for rural, low-income coastal communities as well as an important source of foreign exchange for the economies of developing countries (Wijesekara and Yakupitiyage 2001), and thus have a positive impact in socio-economic terms. Furthermore, it has been argued that displaying corals in private and public aquaria raises public interest and awareness, which may ultimately result in increased conservation efforts (Harriott 2003).

However, the sustainability of the trade has been questioned by a number of authors, who highlight problems such as the over-harvesting of target organisms (Andrews 1990; Chan and Sadovy 1998; Wijesekara and Yakupitiyage 2001), discarding of organisms deemed unsuitable for export by middlemen after collection (Lilley 2001) and generally poor husbandry practices along the supply chain (Green and Shirley 1999; Oliver 2003). Frequently the situation is further exacerbated by the fact that collections mainly take place near airports or other facilities that can adequately handle and transport collected animals, so that relatively few areas are harvested, and the negative impacts as a consequence are concentrated on a few regions (Raymakers 2001). Without adequate management, there is the risk of removing too many corals, as well as breaking colonies not directly targeted, thereby creating rubble capable of causing further damage to the reef environment by abrasion (Table 1). In addition, the great majority of organisms are currently harvested in Southeast Asia, where most reefs are already at risk from anthropogenic activities.

Remarkably, the only published study which attempts to quantify the effect of coral harvesting for the aquarium trade *in situ* dates back to 1984, where coral community parameters were compared at environmentally similar harvested and unharvested sites in the Philippines (Ross 1984). Harvest sites had a 64% reduction in coral cover, a 31% reduction in coral density, and the population structure of a traded species consisted predominantly of small, juvenile colonies.

Table 1 Potential consequences of continuous unsustainable coral collection practices (adapted from Bruckner, 2003).

Potential Impact	**Description**
Effect on target population	Overexploitation, localized extinctions, reduced recruitment
Habitat impacts	Reduced coral cover, diversity and rugosity
Effect on associated species	Loss or destruction of habitat and decreased abundance, biomass and diversity of reef fish, invertebrates and other species
Ecosystem impacts	Increased degradation and thus erosion of the reef structure, associated islands and coastal environments
Socio-economic impacts	Conflicts with other uses/user groups, including traditional uses, fishing, tourism

Population dynamics of target species

The population ecology and life-history characteristics of a species, including factors such as growth, reproduction, recruitment and mortality rates, will affect its potential to replace harvested colonies. Overall, there is very little information available on the population biology of the majority of traded coral genera, with studies conducted to date usually concentrating on common small-polyped species such as acroporids, pocilloporids, poritids and faviids (Connell 1973; Hughes and Connell 1987; Harrison and Wallace 1990; Babcock 1991; Johnson 1992; Connell et al. 1997; Bak and Meesters 1999; Meesters et al. 2001; Adjeroud et al. 2007; Edmunds and Elahi 2007). In addition, the amount of data available is further hampered by the lack of long term studies, which very few authors attempt (but see e.g. Connell et al. 1997; Edmunds and Elahi 2007) since scleractinians are slow growing and have long lives (Harrison and Wallace 1990).

In addition to this general lack of data, the colonial nature of the majority of scleractinians results in a distorted relationship of colony size and age due to processes such as colony fusion, fission and partial mortality (Hughes and Jackson 1980; Babcock 1991). Coral species grow by repeated budding of building blocks known as polyps, which can usually function and survive alone or in small groups when isolated from the rest of the colony (Hughes and Jackson 1985). The sum of all the polyps derived from the same larva, whether situated in one or several separate colonies of clones, makes up the genet (Hughes and Jackson 1985). The resulting complex demographic patterns prevent the application of traditional population dynamic models (Goffredo et al. 2004), except in a few species in which relating size and age is possible. This is for instance the case in corals with compact or massive growth forms, where the original size can frequently be judged from the shape of the living portion (Connell 1973). Similarly, some branching corals rarely fragment or fuse, and any partial mortality can easily be identified by anomalies in the regular growth pattern (e.g. *Pocillopora* spp., Grigg 1984). Additionally, aclonal scleractinian species do exist, and in these solitary corals size and age are directly related. In such species the estimation of growth as well as natural mortality rates and lifespans, and hence ultimately the processes of turnover and recovery needed in stock assessments for exploitation management purposes, are straight-forward (Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003).

The potential for recovery from harvesting activities will to a large extent also depend on the reproductive characteristics of the targeted coral species. Factors such as the impacts of population density reductions on fertilisation successes, the effects of size selective harvesting in species where fecundity and polyp size/age are related or in species which show patterns of sequential hermaphroditism, as well as patterns of larval dispersal ultimately control larval supply to a reef, and thus need to be considered when assessing the capacity for recruitment and population recovery. Functional sexual reproductive patterns that have been described in scleractinian corals are however extremely diverse and complex, and include hermaphroditism/gonochorism, as well as brooding/broadcast spawning species.

Whilst most scleractinians are simultaneous hermaphrodites, developing mature ova and sperm at the same time (Harrrison and Wallace 1990), sequential hermaphroditism, where individuals change sex over their lifetimes or successive breeding seasons, has also been reported (e.g. Glynn et al. 2000). Although there are general family trends, a number of species have complicated sexual patterns, including typically gonochorists which are occasionally hermaphroditic (e.g. *Turbinaria mesenterina*), and species which have equal numbers of males, females and hermaphrodites (e.g. *Agaricia humilis*; Harrrison and Wallace 1990).

The majority of corals are so called spawners, which release gametes into the water for external fertilization and subsequent development. In the less common brooding scleractinians, fertilisation is internal and the planulae develop within polyps (Harrison and Wallace 1990). Both modes of development have been recorded in the majority of families, with contrasting modes of development depending upon geographical location in some cases, (e.g. *Goniastrea aspera*, Nozawa and Harrison 2005). Whilst brooding corals tend to breed and release planulae over extended periods or indeed year-round, spawners usually have more restricted or discrete annual breeding seasons, which often occur synchronously within each population (Babcock et al. 1985). Brooded planulae generally settle within 1-2 days of release, while planulae from spawning corals require 4-6 days after gamete release before they settle and are thus much more likely to disperse over larger distances (Harrison and Wallace 1990).

Because of the inherent difficulties in studying coral larval dispersal pathways *in situ*, most information on larval source-sink dynamics to date has come from the study of the indirect effects of larval dispersal on the gene flow and genetic differentiation among populations (e.g. Ayre and Hughes 2000; Nishikawa et al. 2003; Magalon et al. 2005; Vollmer and Palumbi 2007). However, while quantitative figures on larval flow rates as well as the precise locations of larval origins would be ideal, the data on the genetic differentiation between populations obtained by the application of standard present-day analyses are not as precise, and in addition to present day factors such as the roles of larval dispersal capabilities (Ayre and Hughes 2000; Lourie et al. 2005) and physical oceanographic features (Williams and Benzie 1996; Rodriguez-Lanetty and Hoegh-Guldberg 2002), also may bear traces of historical events (Nelson et al. 2000; Barber et al. 2002). An accurate interpretation of genetic data thus requires knowledge on a species reproductive characteristics, the pathways and strengths of currents in the studied habitat, and needs to be aware that a region's historical developments may be just as important as present day influences (Voris 2000).

Management approaches

In an attempt to protect coral reef resources, many countries currently have severe restrictions on coral harvesting in place, including in many cases a complete prohibition on the collection, sale and export of coral (e.g. the Philippines, Mulliken and Nash 1993). However, the sustainable harvesting of corals is theoretically possible through the application of a number of standard management strategies, including: (1) licensing schemes for both fishermen and trading companies, (2) setting quota limits on the numbers, sizes and taxa of corals collected (3) establishing defined collection sites and no-take zones (3) banning unacceptable collection methods and gear (4) monitoring collection sites as well as control sites for comparative purposes to evaluate resource status / harvest impacts / the success of management strategies (5) establishing eco-labeling schemes to enable consumers to support sustainable harvesting initiatives (Bruckner 2003).

Stock assessment models with the basic purpose of providing advice on the optimum exploitation of a group of organisms with similar growth and mortality parameters in a particular geographic area have a long tradition in fisheries science (e.g. Thompson and Bell 1934; Schaefer 1954; Beverton and Holt 1957; Ricker 1975; Pauly 1984). According to one simple grouping, fish stock assessment models can be divided into so called holistic and analytical models (Sparre and Venema 1998). Holistic models are simple and require only limited data on the stock of interest, such as catch per unit effort, whereas analytic models, developed amongst other authors by Thompson and Bell (1934) and Beverton and Holt (1957) require the age composition of catches to be known, and thus produce more reliable estimates. Although such models originally developed for finfish populations are routinely used to inform invertebrate fishery management decisions (see Caddy 1998 for a review), and their use has in the past been advocated for the ornamental coral trade (Chadwick-Furman et al. 2000; Goffredo et al. 2004), this has not been attempted to date.

The number of corals harvested and subsequently exported from the world's leading exporter, Indonesia, is at present managed through a system of collection quotas. These are set annually for each species and province by the Indonesian Science Institute (LIPI, Lembaga Ilmu Pengetahuan Indonesia), assigned to the Indonesian Coral Shell and Fish Association (AKKII, Asosiasi Koral, Kerang dan Ikan Hias), whose members hold the trading monopoly in the country (Bentley 1998), and are monitored by the Natural Resources Conservation Agency (BKSDA, Balai Konservasi Sumber Daya Alam). Although there are other measures to protect coral reef ecosystems, such as a number of marine protected areas where coral harvesting is not permitted (Bruckner 2002), these are not targeted at managing the coral trade specifically. In Fiji, quotas are established for the operators involved in the live coral trade, and a set of environmentally friendly guidelines for coral harvest and export has been in place since 2004 (Batibasaga 2006). Similarly, the Ministry of Fisheries in Tonga has developed a code of practice for collection which includes quantities and locations of harvest regulated through permits (Bruckner 2002). In contrast, there are no specific regulations, policies or management plans in place as yet in the Solomon Islands (Lal and Kinch 2005).

The international trade in corals is in addition legally regulated by the Convention of Trade in Endangered Species of Wild Flora and Fauna (CITES) agreement, and even in countries which are not signatory such as the Solomon Islands, exports have to comply with the importation rules of CITES member states, which includes European Union countries and the United States. The treaty first listed a number of scleractinian coral species under Appendix II in 1985, and proceeded to include all remaining species in 1990. Ratifying countries can only trade species if export will not be detrimental to their survival. The significance of this legislation is that it forces coral exporting countries to manage coral harvesting activities in such a way that exported species are not threatened: Fiji for instance had its entire international trade in corals suspended in 2002 as it did not demonstrate a commitment to protecting traded organisms. Similarly, the EU is currently banning the import of a number of rare coral species from Indonesia (*Euphyllia cristata*, *E. divisa*, *E. fimbriata*, *E. picetti*, *Scolymia vitensis*), Tonga (*Acanthastrea* spp., *Cyanarina lacrymalis*, *Favites halicora*, *Platygyra sinuosa*, *Scolymia vitensis*), Fiji (*Blastomussa wellsi*, *Plerogyra simplex*, *Trachyphyllia geoffroyi*) and the Solomon Islands (*Heliopora coerulea*, *Catalaphyllia jardenei*), stating a lack of biological data and thus arbitrary basis of current export quotas as a reason for prohibiting imports (Raymakers 2002; Jones, 2008). Unfortunately, designing scientifically sound management plans for the great majority of corals traded by the aquarium industry will remain unfeasible as long as knowledge about their ecology and life history characteristics is as limited as it is to date.

Thesis aims

The aim of this thesis is to address the poor scientific foundation upon which present day ornamental trade management regimes are based using a multi-disciplinary case-study approach. Specifically, the objectives of the study are to:

(1) Characterise life history parameters for a coral species of major importance in the international live coral trade
(2) Understand the socio-economic aspects of the aquarium trade in a coral species of major importance
(3) Obtain quantitative estimates of the effects aquarium collectors are having on a coral population
(4) Explore the application of traditional finfish stock assessment models to coral fisheries
(5) Review current management regimes and potential future options based on the findings

Thesis structure

An overview of the materials and methods used to address these objectives, and a discussion of the general results is presented below. Three scientific papers based on data collected over the course of this study, which all contribute in different ways to the overall aim of increasing the scientific knowledge available for the future development of live coral trade management strategies (Table 2), are presented in Chapters 2-4.

Table 2 Overview of the specific objectives addressed by the scientific papers included in the present thesis.

Topics Covered	Paper Number	Chapter Number
Coral life history parameters	I, II	II, III
Socio-economics of aquarium trade	III	IV
In situ effects of aquarium trade on corals	III	IV
Application of stock assessment models	I, III	II, IV
Coral trade management recommendations	I, II, III	II, III, IV

Summary of materials & methods

Study area

Indonesia is a vast archipelago of over 17000 islands situated between the eastern Indian Ocean and the western Pacific, with landmasses and shallower seas acting as both a barrier and a connection between the two ocean basins. The region is characterised by a variety of highly productive coastal ecosystems including mangrove forests, extensive seagrass beds, resource rich pelagic environments as well as vast expanses of coral reefs, which support one of the largest marine fisheries in the world (Hopley and Suharsono 2000). Moreover, the Indonesian coastal zone supports around 60% of the country’s estimated 200 million people (Burke et al. 2002), and although human interactions with coral reefs in Indonesia date back to prehistoric times (Soegiarto and Polunin 1981), the unsustainable use of resources has risen dramatically as a result of the increasing demands of growing populations, international trade and changing consumption patterns over past decades (Miclat et al. 2006). Cyanide fishing for the live food and aquarium fish trades, blast fishing, coral mining for construction materials and the aquarium trade, land-based pollution and general overfishing have had considerable cumulative impacts on local reefs over time, with only an estimated 23 and 45% of reefs remaining in good condition (live coral cover of >50%) in western and eastern Indonesia respectively (Hopley and Suharsono 2000).

The Spermonde Archipelago off the coast of Makassar in South Sulawesi extends about 60 km offshore, and consists of about 150 islands with fringing reefs as well as a large number of barrier and submerged patch reefs (Tomascik et al. 1997). An estimated 6500 fishing households are scattered over the islands and depend upon the reefs for their livelihoods, with a lack of employment alternatives outside the fishery causing fishing efforts to remain high throughout the year (Pet-Soede et al. 2001). Reef degradation is widespread (Edinger et al. 1998), with little recent improvements in management strategies despite warnings that the reef ecosystem may be on the verge of collapse voiced by scientists over 10 years ago (Erdmann 1995). Corals are selectively harvested over large areas for the aquarium trade in Spermonde (Bruckner 2002), which, in part due to the proximity to Makassar airport, is one of four major coral collections sites in Indonesia (Raymakers 2001).

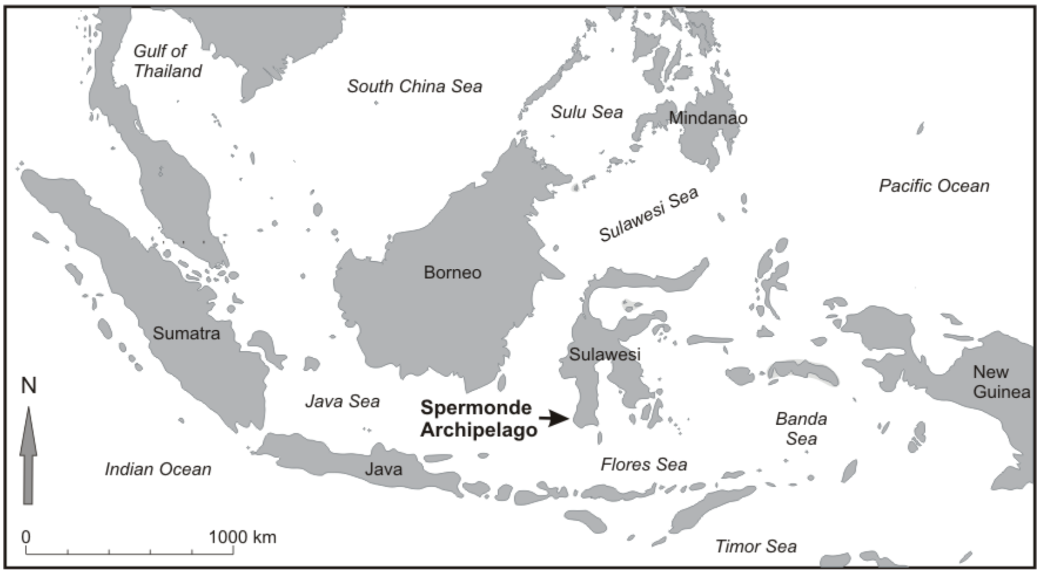


Fig. 2 Location of Spermonde Archipelago within the Indo-Malay Archipelago.

Study organism

The mushroom coral *Heliofungia actiniformis* ranks among the top five of all coral species being exploited for the global live coral market (Green and Shirley 1999), and has had the highest trade quotas in South Sulawesi since 2004 (BKSDA Makassar 2008). Its popularity stems primarily from its large and frequently brightly coloured tentacles, which are extended day and night. In addition, whilst most scleractinian coral species remain fixed to the substratum, 36 of 41 species in the familiy Fungiidae, including *H. actiniformis*, dissolve part of their skeleton and detach to become free living individuals as an integral part of their life history (Hoeksema 1989), which makes collection and handling of this species easy (Yamashiro and Yamazato 1987).

To date, scientific knowledge on the ecology of *H. actiniformis*, whose distribution is limited to the Indo-West Pacific, is limited to studies conducted in Palau on post-larval development (Abe 1937), polyp growth (Abe 1939), polyp mobility (Abe 1940), and to records of field observations throughout the Indonesian Archipelago (Moll 1983; Hoeksema and Moka 1989, Hoeksema 1990).

Population dynamics

H. actiniformis growth rates as well as the relationship between polyp length, width and skeletal mass were measured at a nearshore site in the Spermonde Archipelago for polyps spanning the entire size range of this species. Growth was expressed according to the von Bertalanffy growth model (von Bertalanffy 1938), and a growth performance index subsequently calculated (Munro and Pauly 1983). *H. actiniformis* size-frequency distributions, the abundance of life cycle stages and the characteristics of habitat substratum were assessed by belt transects at three replicate unharvested sites, and natural mortality rates calculated for the different life cycle stages by applying a length-converted catch curve analysis (Pauly 1984). Size-frequency distributions were converted to age-frequencies distributions based on the relationship between coral length and growth (von Bertalanffy 1938). To examine the relative importance of sexual and asexual reproduction, all polyps sized 0-4 cm within the belt transects were re-counted every 6 months over an 18 month period. All attached polyps found during initial sampling were in addition marked and the recruitment of newly settled sexual larvae recorded over a 12 month period.

To complement these *in situ* surveys an investigation into larval dispersal patterns was carried out: partial rDNA sequences of *H. actiniformis* (ITS1-5,8S-ITS2) were determined for ten sites throughout the Indo-Malay Archipelago, as well as nearshore, midshelf and outershelf reefs in the Spermonde Archipelago. Levels of genetic variation within/between populations, as well as potential population groupings were subsequently tested according to geographic and oceanographic affinities. An isolation by distance analysis was carried out to determine whether there was an association between levels of genetic similarity and geographic distances (after Wright 1943), and haplotype/nucleotide diversity indices as well as a haplotype network were calculated to identify further clues towards the most likely historical/present day explanations for the observed patterns of genetic variability.

Socio-economics

In order to fully understand the on-site circumstances and appropriately interpret the results of the ecological data in terms of management implications, an appraisal of the socio-economic aspects surrounding the trade in *H. actiniformis* was carried out. Government statistics regarding numbers of companies, licensed fishermen and location of holding tanks were obtained from the Makassar Natural Resources Conservation Center (BKSDA, Balai Konservasi Sumber Daya Alam, 2006). In addition fishermen were interviewed about harvesting practices using a semi-structured questionnaire survey, and whenever possible *H. actiniformis* polyps in holding tanks destined for sale were examined.

Harvesting impacts

In order to look at *in situ* impacts of the trade, population demographics at three replicate harvested sites were measured using the same methods previously employed at the unharvested sites. Total mortality rates were now calculated separately for the attached polyps, free-living polyps being exploited by the aquarium trade, and larger free living polyps no longer targeted by fishermen, again by applying a length-converted catch curve analysis to the length-frequency data (Pauly 1984). To further describe fishery dynamics, fishing mortality rates (F) were calculated by subtracting natural mortality rates (M) at unharvested sites from total mortality rates (Z) at harvested sites. Exploitation rates (E) were subsequently obtained from F/Z (Gulland 1971).

Application of stock assessment models

Based on the above data, unharvested, natural *H. actiniformis* populations were described by the application of a modified version of the Beverton and Holt (1957) yield per recruit model: an age-specific cohort biomass curve was generated using the polyp growth curve, the relationship between polyp skeletal mass/length, and the average of the natural mortality rates calculated above (after Grigg 1984; Chadwick-Furman et al. 2000; Tsounis et al. 2007). The age at maximum production of a year class, and thus theoretical optimal size and age for harvest, was thus estimated. Subsequently, maximum potential economic yield per recruit was determined by adding economic values to this yield per recruit model. Yield predictions were then calculated by an aged-based Thompson and Bell (1934) model (1) according to the current situation (2) with fishery mortality values below and above present levels and (3) after the hypothetical introduction of a 5 cm size limit.

Overview of results and general discussion

Population dynamics

Results revealed relatively fast growth rates of ~1.2 cm yr^{-1} for the young, attached *H. actiniformis* polyps. Growth however slowed as corals aged, and a linear relationship between growth rates and polyp length was found, indicating non-seasonal von Bertalanffy type growth. The growth performance index was low relative to related mushroom coral species, indicating that *H. actiniformis* is slow to attain its final body size and thus likely to be vulnerable to overexploitation (**Paper I**). Similar data on growth performances is at present not available for comparative purposes from scleractinian families besides the Fungiidae, which is partly due to the colonial nature of many other species, where maximum size is difficult to ascertain.

H. actiniformis population structure was characterised by a marked decrease in the frequency of individuals with age, with high mortality rates for the attached life cycle stage contrasted by mortality rates an order of magnitude lower for detached polyps. The repeated production of stalks from a single sexual recruit was the main mode of asexual reproduction in *H. actiniformis*, and responsible for the high abundance of young polyps (**Paper I**). Such prolific budding by reef stalks seems to be unique to this species, with sexual recruits of other mushroom corals usually only producing a single stalk capable of regenerating tentacles (Chadwick-Furman and Loya 1992). Larval recruitment monitoring showed only a very limited number of sexual recruits at all sites over both sample intervals (**Paper I**). The facts that natural mortality rates of attached stages was so high, and that the successful recruitment of sexual larvae was rare over the study period, highlight the importance of prolific asexual reproduction in the maintenance of *H. actiniformis* populations in Spermonde. Examples of coral species where asexual reproduction through budding or fragmentation play important roles include for example *Acropora aspera*, *A. cervicornis*, *Poritis compressa*, *P. lutea*, *Pocillopora damicornis*, *Madracis mirabilis* and *Fungia* spp. (Highsmith 1982), but for many of the traded species data on the relative importances of sexual vs. asexual reproduction are lacking.

Although there was no statistically significant difference in mortality rates of detached polyps at the three sites surveyed, only few polyps survived to an estimated age of 40 years at the two sites with high rubble cover. The unstable nature of coral rubble as a substrate may have primarily impacted the survival rates of the largest polyps: while *H. actiniformis* polyps of 6-10 cm are able to inflate their tissue and overturn to a normal position when turned upside down as shown by Abe (1939), larger polyps may be unable to overturn due to the exponential increase in skeletal weight with polyp length (**Paper I**).

Increasing abundance of coral rubble on reefs in the Spermonde Archipelago has been an issue for years (Erdmann 1995; Pet-Soede and Erdmann 1998), and its causes clearly need to be addressed if coral reef resource exploitation of any type is to continue in the future. The significance in terms of *H. actiniformis* population dynamics is that if fewer reproductively mature corals are able to survive on unstable substrates, there will be less larval input to the system, an issue which has to be taken into consideration when assessing the viability of spawning stocks at harvested sites (**Paper III**). Exacerbating this correlation is the fact that previous studies of solitary corals have shown a strong size-dependency of fecundity (Goffredo et al. 2002; Waller et al. 2002), so that the relationship between the number of larvae released and the number of reproductively mature polyps present on a reef is unlikely to be linear.

However, to fully understand the situation, knowledge of larval distribution as well as the potential for larval input from surrounding reefs is needed. A slight, but significant genetic structure was found within the Spermonde Archipelago, with an average distance over which dispersal was limited of 52 km (**Paper II**). The data followed the isolation by distance model, which indicates that geographic separation is an important factor for the degree of larval connectivity between populations. Indeed, a previous study on the reproductive characteristics of *H. actiniformis* found that well developed, brooded larvae were released by the mother polyps, the great majority of which had attached to the substrates provided in the laboratory after 3 days (Abe 1937), suggesting limited larval dispersal potential. However, local current patterns were also important in shaping larval flow pathways: there was a lack of genetic structure between the outershelf and midshelf populations which are influenced by the strong currents passing through the Strait of Makassar, but limited gene flow between the shallower nearshore and midshelf sites less influenced by the offshore currents. Furthermore, whereas a number of private haplotypes were found in the nearshore populations, none were present at the midshelf and outershelf sites. Although it is not possible to provide exact quantitative data on larval exchange between sites with the methods used here, such private haplotypes are most likely to develop in populations which have a limited exchange of larvae with surrounding populations (Barber et al. 2006). Based on these results it is thus likely that potential spawning stocks at unharvested nearshore sites will only provide a limited input of larvae to harvested mid- and outershelf populations and vice versa (**Paper III**). There are no comparative studies on other coral species available for Spermonde, although previous work on the genetic structure of the giant clam *Tridacna crocea* (Nuryanto and Kochzius 2006) and the stomatopod *Haptosquilla pulchella* (Barber et al. 2002) found panmixia of larvae throughout the archipelago. However, both species have significantly longer planktonic larval phases: 7-10 days for *T. crocea* (Lucas, 1988) and 4-6 weeks for *H. pulchella* (Barber et al. 2002), and similar patterns may be expected for spawning scleractinian coral species.

At the large scale of the Indo-Malay Archipelago, long-distance gene flow between the Central Visayas and populations as far away as those in the Flores Sea was contrasted by regionally isolated populations in New Guinea, Tomini Bay, and the Java Sea (**Paper II**). The presence of one large population with only limited genetic structure spanning the central part of the Indonesian Seas further supported the importance of the oceanographic impact on *H. actiniformis* larval dispersal: all populations were very close to or directly in the path of the Indonesian Throughflow (ITF) current. In terms of haplotype and nucleotide diversity, more diverse populations were also found in areas of presumed current and thus larval mixing. Biologically, such large scale dispersal is made possible by the fact that although the larvae of brooding corals settle faster than those of broadcast spawners, their potential maximum competency periods are much longer due to the high energy reserves they can draw upon when needed (Richmond 1989; Wilson et al. 1998). Similarly, a previous study of a the brooding coral *Pocillopora damicornis* found that larvae frequently settled close to parent colonies, whilst a proportion remained competent and planktonic for long periods (Ayre 1997).

However, it is unlikely that a single larva drifted all the way from the Philippines to the Flores Sea. Instead, the significant isolation by distance analysis at the scale of the entire Indo-Malay Archipelago indicated that dispersal is occurring via a series of stepping stones (Kimura and Weiss 1964). Whereas the isolation of the populations in New Guinea and Tomini Bay could be explained by the lack of such stepping stones and connecting currents respectively, the genetic break between the neighbouring Java and Flores Sea *H. actiniformis* populations was surprising, given the presence of seasonally reversing currents in this region. The most likely explanation is that these populations still carry the genetic signature of re-colonisation events on the Sunda Shelf at the end of the last glacial period, which had left this region completely exposed (Voris 2000). The revealed pattern of two major haplotype clades suggests that this re-colonisation after the Pleistocene may have come from the Indian Ocean.

Table 3 Overview of population genetic studies carried out to date for the top ten traded scleractinian coral genera in 1998-2005 (Wabnitz et al. 2003; Jones 2008); no data available for *Catalaphyllia* sp., *Euphyllia* spp., *Favia* spp., *Goniopora* spp., *Lobophyllia* spp., *Montipora* spp., *Plerogyra* spp., *Porites* spp., *Trachypyllia* spp., *Turbinaria* spp.

Species	Locations, scale (km)	Marker	Inferred levels of gene flow	Ref.[1]
Indo-Pacific				
Acropora cuneata, *A. hyacinthus*, *A. millepora*, *A. palifera*, *A. valida*, *A. cytherea*	Australia, 1-8, 1200	Allozymes	Limited gene flow within reefs, but enough larvae dispersed for large scale panmixia over entire Great Barrier Reef (GBR)	1
A. cuneata, *A. valida*	Australia, 700, 1200	Allozymes	Panmixia over 1200 km of GBR, isolation of island 700 km away	2
Acropora palifera	Australia, ~1	Allozymes	Panmixia	3
Acropora nasuta	Australia, 5, 35, 500	Msats, introns	Significant structure on large and medium scales, panmixia within reefs	4
Acropora tenuis	Japan, 30-150, 500	Allozymes	High gene flow at small scale, limited gene flow at large scale	5
Acropora aspera, *A. digitifera*	Australia, 6.5-155	Allozymes	Restricted gene flow, mating between close relatives	6
Heliofungia actiniformis	Indonesia, Philippines	ITS	Significant structure at large and small scales, affinities of populations connected by currents	7
Caribbean				
Acropora palmata	up to ~2600	Msats	Very limited gene flow between eastern & western Caribbean, high flow within regions	8
Acropora cervicornis	<100, 500, 2500	MtDNA, introns	Dispersal over moderate/long distances limited, lack of structuring in 17 of 20 populations at fine scale	9

[1] References: (1) Ayre & Hughes 2000; (2) Ayre & Hughes 2004; (3) Benzie et al. 1995; (4) Mackenzie et al. 2004; (5) Nishikawa 2003; (6) Whitaker 2004; (7) Knittweis et al. 2008 (**Paper II**); (8) Baums et al. 2005.; (9) Voller & Palumbi 2007.

Whilst the only comparable data available is from studies of different geographic areas/species (Table 3), and the confounding influence of historical factors needs to be considered as evidenced by the population genetic structure found for the Sunda Shelf, larval seeding of neighbouring reefs by *H. actiniformis* in the presence connecting currents has several management implications. Firstly, harvesting at both upstream and isolated populations should be restricted since the limited larval input from elsewhere is likely to result in slower recovery rates from over-harvesting. In particular the protection of upsteam sites such as the Philippines and North Sulawesi should be a priority since these may serve as important larval source regions. Indeed, high levels of gene flow have previously been found along the path of the ITF, from North-Eastern Borneo to Southern Sulawesi for the prawn *Panaeus monodon* (Sugama et al. 2002), from Northern Sulawesi/Northern Borneo to South Sulawesi for the boring giant clam *Tridacna crocea* (Nuryanto and Kochzius 2006), from Northern Sulawesi to the Flores Sea for the stomatopods *Haptosquilla glyptocerus* and *Gonodactylinus viridis* (Barber et al. 2006), and from Cebu in the Philippines to West Timor for the pink anemonefish *Amphiprion perideraion* (Hamid 2007).

However, as illustrated by the small scale pattern of genetic structuring within the Spermonde Archipelago, where larval input via the ITF currents is more likely for mid- and outershelf reefs than the more isolated nearshore sites, the detailed characteristics of each harvesting area also need to be taken into account (**Papers II, III**).

Socio-economics

The questionnaire on *H. actiniformis* fishing practices revealed very distinct collection criteria driven by consumer demand, with brightly coloured polyps small enough to fit into home aquaria and easy to transport as the main target of fishermen in Spermonde. Fishermen only receive about 30-70 US$ cents (depending on size) for the most expensive colour morphs. Although a few companies employ fishermen who exclusively collect corals, more frequently fishermen opportunistically collect whatever they can, including fish, sea cucumbers and coral/ornamental fish for the aquarium trade. Middlemen subsequently choose which pieces to buy, while the rest is discarded (**Paper III**). It seems at least part of the trade is clandestine at the moment: it was impossible to gain access to holding tanks in order to monitor polyp landings and thus adherence to the set quotas except for a few occasions. In addition many of the fishermen did not have the licenses required by Indonesian law, and admitted avoiding police controls (**Paper III**).

A useful theoretical framework to visualise the difficulties faced by managers is arguably the classic Schaefer yield curve (Schaefer 1954). It proposes that with increasing fishing efforts the exploitation of a resource will initially produce increasing yields, until a point where the resource is fully exploited, when catch per unit effort begins to decline. Eventually the fishery is no longer viable as costs exceed income (Fig. 3).

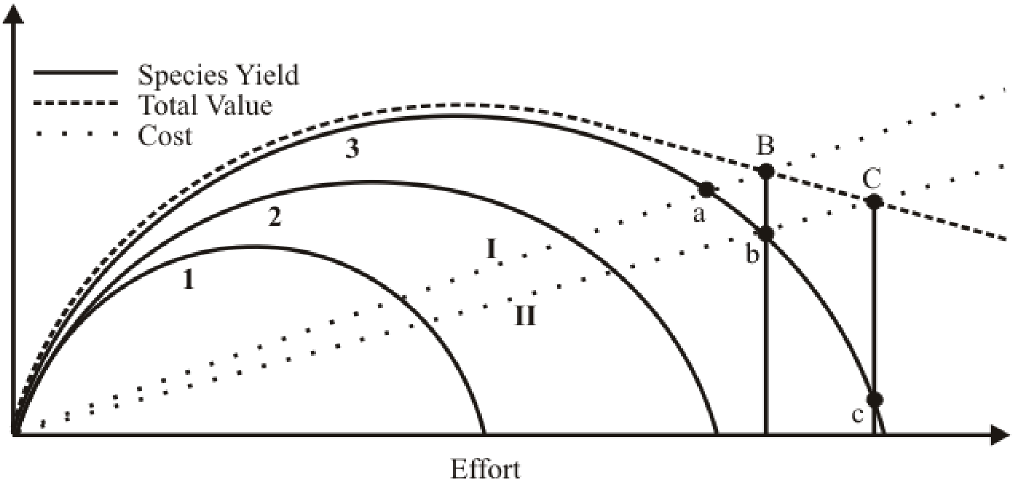


Fig. 3 Curves of biomass yield (based on the Schaefer yield curve), total value and cost lines with increasing effort. Fishing is no longer viable where the cost and value curves intersect. Normally total value mirrors total biomass yield, and the cost (**I**)/value curves intersect at point **a**. If value increases with rarity, total value will decline at a slower rate and diverge from the yield curve, and the cost/value curves intersect at point **B**, which maps onto effort point **b** as the economic equilibrium point. In fisheries where costs are lowered by the provision of subsidies, the new cost line (**II**) could conceivably intersect the total value curve at point **C**, which maps onto effort point **c**, where the fishery is severely overexploited. The effort at which fishing stops will depend on which species is the driving force (three species are represented here). For example, a situation where the fishery is based on species **3** would result in overfishing of all species and effectively eliminate species **1** and **2**. Adapted from Sadovy and Vincent (2002).

However, the Spermonde ornamental trade fishery is a multispecies fishery, not only driven by the yield for effort ratio of *H. actiniformis* alone, but by the additive effects of a number of species (**Paper III**). A number of high-return organisms such as *Trachyphyllia geoffrei* and *Catalaphyllia jardinarei*, as well as species such as sea cucumbers and food fish, made trips economically viable for fishermen. Additionally prices for coral traded in the aquarium industry frequently rise as rarity increases (Wabnitz et al. 2003), which means fishing will remain profitable even in a high effort and low catch situation (Fig. 3). A lack of alternative income possibilities in many cases also means the benefits of earning a small income from fishing for the ornamental trade by far outweigh the alternative of not earning a living at all (Reksodihardjo-Lilley and Lilley 2007). Furthermore, heavy fuel subsidies by the Indonesian government combined with the provision of materials needed for harvesting such as fins, masks, air compressors/SCUBA tanks etc. by local companies considerably lower costs to fishermen (**Paper III**). Overall, opportunity costs (rewards to be gained from working elsewhere) are thus very low, and the risk for the aquarium trade to overexploit reef organisms as a direct consequence are high (Fig. 3).

The Indonesian system of license restrictions for both companies and fishermen trading in live corals to avoid such overharvesting unfortunately seems unlikely to succeed based on the present findings. Whilst the 10 companies which were operating in June 2006 were successfully guarding their territory against any newcomers, the large number of fishermen, which were at least partly operating at subsistence level and only contributing a limited number of coral pieces each, currently makes the license system impractical to impose (**Paper III**).

The questionnaire surveys also revealed a lack of knowledge and awareness about the basic biological features of *H. actiniformis*: attached clusters are routinely harvested, but only the largest polyps (which have already developed a flat base) are kept, whilst the rest is discarded on site. Occasionally entire clusters are sold to middlemen as *Euphyllia glabrescens*: due to the similarity of the tentacles and early growth morphology of *H. actiniformis* it is difficult to tell the two species apart. Indeed, when shown pictures of attached *H. actiniformis* and small colonies of *E. glabrescence*, none of the fishermen/middlemen interviewed could distinguish these (**Paper III**). As a consequence, not only are the attached stages unable to fulfill their function of providing a continuous input of young polyps to the reef (**Paper I**), but a considerable portion of harvested *H. actiniformis* polyps is never included in quota statistics. The full extent of such discarding and mislabeling is unknown at present, although the accuracy of trade data for the aquarium industry in general has in the past been criticized by a number of authors (Wabnitz et al. 2003; Jones 2008). The results of the present study for the first time illustrate that mislabeling and under-reporting in fact starts right at the bottom of the supply chain.

Harvesting impacts

Comparing *H. actiniformis* population structures surveyed at harvested sites (**Paper III**) and unharvested sites (**Paper I**) revealed (1) a marked decline in the overall abundance of polyps at harvested sites, particularly in young, attached polyps and (2) significantly higher total mortality rates for polyps in the 0-4 and 4-11 cm size classes. The severely reduced abundance of young, attached *H. actiniformis* compared to natural populations (**Paper I**) reflects the results of the socio-economic surveys. Since there is panmixia of larvae among harvested and unharvested nearshore sites (**Paper II**), localised stock-recruitment effects are unlikely to have an impact on local recruitment patterns.

The calculated exploitation rates however showed that whilst polyps sized 0-11 cm are being targeted by the fishery with E = 0.1, the main fishing pressure is on corals measuring 4-11 cm in length, where fishing mortalities exceed natural mortalities so that E = 0.7. As a result of such high fishing pressure only very few polyps surviving to a size larger than 11 cm were found at harvested sites. Since *H. actiniformis* becomes reproductively mature at an estimated size of 10 cm (Abe 1937), this means that with current fishing pressure polyps rarely survive to an age where they attain reproductive maturity. In addition, those polyps that were found all had a dull brown colour, and thus no commercial value (**Paper III**).

Overall, there were thus a number of indicators that current quotas are too high. Although the remaining brown polyps may in fact prevent *H. actiniformis* from being harvested to local extinction, their larval input into the system may not necessarily help to ensure long term trade sustainability: whilst little is known about the heredity of coral colour to date, it seems that genetic differences ultimately determine the differences between colour morphs (Takabayashi and Hoegh-Guldberg 1995). The dangers of recruitment overfishing might thus be even more severe than it appears at first glance.

Application of stock assessment models

According to the estimates calculated by the application of the Beverton and Holt yield per recruit model (1957), the minimum harvest size for *H. actiniformis* in Spermonde should be 12-13 cm, corresponding to an age of about 20 years. Due to the low natural mortality rates of detached polyps, *H. actiniformis* reaches the point of maximum biomass yield/recruit significantly later than related mushroom coral species (5-14 years), making it more vulnerable to overexploitation. Setting a harvesting size limit of 13 cm would in theory allow to maximise the production of biomass, and have the benefit of allowing for a 7 year reproduction buffer period for polyps (**Paper I**). However, when put into perspective by considering market demands, which unfortunately are for young polyps sized 4-11 cm that fit into standard home aquaria and are easy to transport, this approach is clearly not viable (**Paper III**). This is a significant insight: although never in fact applied to the live coral fishery to date, the application of this model to the estimation of optimal harvest sizes for ornamental species has in the past been advocated by a number of authors (Chadwick-Furman et al. 2000; Goffredo et al. 2004). Whilst it may be applicable to coral species where it is feasible to harvest large colonies in order to split these into fragments small enough for sale, a situation to the one encountered in this study will be found for other species where the splitting of polyps/colonies is not possible, including *Trachyphyllia geoffroyi*, *Catalaphyllia jardinei*, *Cynarina lacrymalis*, *Herpolitha limax, Fungia fungites*, *F. moluccensis*, *F. paumotensis*.

Instead the utility per recruit paradigm seems more suited to the development of potential guidelines regarding optimum harvest sizes in such species. In *H. actiniformis*, economic yield per recruit based on natural mortality rates (**Paper I**) as well as prices paid for the different sizes of polyps peaked at an age of 5 years and a corresponding size of ~5 cm, with 4.19 US$ cents per recruit (**Paper III**). A subsequent application of the Thompson and Bell model revealed that relative to the current situation, a decrease in fishing mortalities by 20% would in fact provide similar profits, and that the introduction of a 5 cm size limit could increase profits since both measures would counteract present day growth overfishing. If quotas were to be set at a level where fishing mortalities were not to exceed natural mortalities, a 60% decrease of fishing efforts for polyps sized 4-11 cm relative to the current situation would be needed. In combination with the introduction of a 5 cm size limit, this could in fact be achieved without lowering profits (**Paper III**). Moreover such a size limit would put an end to the practice of harvesting attached polyps, avoid the discards being made at the moment, and allow the attached phases to provide the continuous input of young polyps so important in natural *H. actiniformis* populations (**Paper I**).

For such stock assessment models to be valid, two major assumptions have to be met however: (1) that harvest does not affect recruitment rates (2) that populations are in a steady state. In the present case-study the first assumption seems to hold for the sites studied: despite the limited number of reproductively mature polyps remaining at harvested sites (**Paper III**), larval flow took place within nearshore sites (**Paper II**), and thus mature polyps from unharvested sites can be presumed to maintain recruitment rates at the harvested sites.

However, this will not be the case for harvested sites in the mid- and outershelf regions of the Spermonde Archipelago, where the trade is concentrating its fishing efforts (**Paper III**). Secondly, the under-representation of polyps aged 30-45 years at the two unharvested sites with high rubble cover (**Paper I**) challenges the second assumption. Since there were no statistically significant differences in overall mortality rates at the three unharvested sites (**Paper I**), it appears the models may hold at present, but only as long as reefs are not degraded further and polyps are exposed to even higher rubble cover and more unstable reef slopes. Overall it is thus vital to direct management efforts towards the protection of *H. actiniformis* spawning stocks as well as this species' habitat, for instance through the establishment of functional marine protected areas. Whilst fish stock assessment models can be powerful tools to advise managers of optimum harvesting strategies, long term sustainability can only be achieved if model assumptions are addressed and sufficient ecological data is available to decision makers for the species in question.

Conclusions

The combination of a variety of methodological approaches and scientific disciplines to study the trade in *H. actiniformis* provided a unique opportunity to assess current management challenges and their potential solutions. The research on life history parameters revealed a low growth performance index, a late reproductive maturity at ~10 years, larvae capable of large distance dispersal yet prone to local isolation in the absence of strong currents, and a unique asexual reproduction life-phase subjected to high natural mortality rates. In combination with a number of unfavourable socio-economic factors including high consumer demands for immature polyps, management policies based on convenience rather than scientific data, a lack of alternative livelihoods for fishermen, and poorly enforced management strategies, the situation is at present leading to the overexploitation of *H. actiniformis* stocks in Spermonde. While information similar to that collected in the present study is lacking for the remaining coral species currently being harvested in Spermonde Archipelago, similar patterns of overexploitation are likely, potentially placing the livelihoods of those depending on the coral trade at risk.

The assessment of the present situation thus shows that license restrictions, quotas and indeed international attempts at protecting corals from overexploitation such as the CITES agreement are at present unfortunately little more than pretence, albeit with huge potentials for future improvements. An application of fisheries stock assessment models showed that whilst the Beverton and Holt yield per recruit model will only be applicable to certain coral growth forms, there is indeed scope for the future use of such models by the aquarium industry. In particular the combination of calculating ideal harvesting sizes and exploring the effects of alternative size limits revealed a simple management strategy with potentially great effects in the present case study: the introduction of a 5 cm size limit. It is conceivable that analogous studies of other exploited species would reveal similarly simple yet effective management strategies. Finally, an issue of paramount importance which emerged several times over the course of this study is the protection of spawning stocks. While the presence of dull colour morphs with no commercial value will protect *H. actiniformis* from being harvested to local extinction, this will do little to ensure trade sustainability, and is unlikely to be the case for most of the remaining coral species. In addition to generally reducing the numbers of corals harvested, the establishment of marine protected areas should be encouraged to achieve this since such no-take zones would function as refuges not only for *H. actiniformis*, but for the multitude of species for which scientific knowledge is as yet too limited to assess the appropriateness of current and potential future management policies.

Outlook

A number of unresolved issues which were outside the scope of the present investigation remain. First of all the current study focussed on only a single coral species out of the 75 species Indonesia exported in 2006. Similar investigations of other species need to be carried out if viable management strategies are to be developed for the industry as a whole. Since such an endeavour would almost certainly cost more than the profits being made and take far too much time, representative species in the most important coral families could initially be chosen for study instead. Besides generally characterising the population dynamics of harvested species, the unresolved issues raised by the present study should be focal study topics, including (1) the role played by size/age dependent levels of polyp/colony fecundity in a species' life history (2) to what extent the expression of colour is a genetic or an acquired trait in scleractinians (3) the implications of general coral reef degradation patterns on the population dynamics of coral species important in the ornamental trade.

A topic whose investigation would benefit not only ornamental trade managers but the wider scientific community is the further study of population genetic connectivity patterns of scleractinian coral species in the Indo-Malay Archipelago. Considering the region's importance as the world's coral biodiversity hotspot (Hughes et al. 2002), the continuing debate on the evolutionary processes which have shaped it (Hoeksema 2007) and the urgent need for effective management of Indonesian coral reefs, it is in fact astonishing that the present investigation is the first to study population connectivity patterns of a coral species in the region. In addition to a general study of coral population genetics, capable of providing data vital in the design of effective marine protected area networks, the study of direct quantitative estimates of larval dispersal rates, and the identification of the precise natal origins of marine species should be attempted in the future (see Jones et al. 2005 for a recent example).

Another subject likely to produce important insights not only for ornamental trade managers but coral ecologists in general is the application of stock assessment models. The application of such models has to date been mainly limited to aclonal, free-living species, including the present study. However, in coral species which rarely fragment or fuse, any partial mortality is obvious as an anomaly in the regular growth pattern and the application of such models is feasible, as Grigg indeed demonstrated for *Pocillopora verrucosa* (1984).

Finally, without further study of the socio-economic parameters governing the live ornamental trade supply-chains and the livelihoods of fishing communities in particular, management attempts, however well informed and diligently designed, are unlikely to succeed. Whilst a detailed appraisal of socio-economic research needs clearly lies outside the scope of this summary, the general topics to be addressed include patterns of governance, the existence of formal and informal institutional arrangements governing the ornamental trade, the functioning of trade and patronage networks, local knowledge and perceptions towards the biological asset bases being exploited, livelihood strategies, their vulnerability contexts and potential alternatives, as well as the arguably more holistic approach of identifying key feed-back loops and resilience thresholds in the socio-ecological system as whole.

References

Abe, N., 1937. Post-larval development of the coral *Fungia actiniformis* var. palawensis Doederlein. Palao Trop. Biol. Station Stud. 1, 73-93.

Abe, N., 1939. Migration and righting reaction of the coral, Fugia actiniformis var. palawensis Doederlein. Palao Trop. Biol. Station Stud. 4, 671-694.

Abe, N., 1940. Growth of Fungia actiniformis var. palawensis Doederlein and its environmental conditions. Palao Trop. Biol. Station Stud. 5, 105–145.

Adjeroud, M., Pratchett, M.S., Kospartov, M.C., Lejeusne, C., Penin, L., 2007. Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. Hydrobiologia 589, 117-126.

Andrews C., 1990. The ornamental fish trade and conservation. J. Fish. Biol. 37, S53-S59.

Ayre, D.J., Hughes, T.P., Standish, R.J., 1997. Genetic differentiation, reproductive mode, and gene flow in the brooding coral *Pocillipora damicornis* along the Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 159, 175-187.

Ayre, D.J., Hughes, T.P. 2000. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54, 1590-1605.

Ayre, D.J., Hughes, T.P. 2004. Climate change, genotypic diversity and gene flow in reef-building corals. Ecol. Lett. 7, 273-278.

Babcock, R.C., 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol. Monogr. 61, 225–244.

Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver J.K., Wallace, C.C., Willis, B.L., 1985. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90, 379-394.

Bak, R.P.M., Meesters, E.H., 1999. Population structure as a response of coral communities to global change. Amer. Zool. 39, 56-65.

Barber, P.H., Palumbi, S.R., Erdmann, M.V., Kasim, Moosa, M. 2002. Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. Mol. Ecol. 11, 659-674.

Barber, P.H., Erdmann, M.V., Palumbi, S.R., 2006. Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. Evolution 60, 1825-1839.

Batibasaga, A., 2006. Members report on the activities of the International Coral Reef Initiative (ICRI), Fiji. ICRI General Meeting, Coxumel, Mexico, 22-23 October 2006.

Baums, I.B., Miller M.W., Hellberg M.E., 2005. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Mol. Ecol. 14, 1377-1390.

Bentley, N., 1998. An overview of the exploitation, trade and management of corals in Indonesia. Traffic Bull.17, 67–78.

Benzie, J.A.H., Williams S.T., 1995. Gene flow among giant clam (*Tridacna gigas*) populations in Pacific does not parallel ocean circulation. Mar. Biol. 123, 781-787.

Beverton, R.J.H., Holt, S.V., 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food Ser. II 19, 1-553.

Bruckner, A.W., 2002. Proceedings of the international workshop on the trade in stony corals: development of sustainable management guidelines. NOAA Technical Memorandum NMFS-OPR-23, Silver Spring, MD, 152 pp.

Bruckner, A.W., 2003. Sustainable management guidelines for stony coral fishereies. In: Cato, J.C., Brown C.L. (eds.), Marine ornamental species: collection, culture and conservation. Iwoa State Press, 167-182.

Burke, L. Selig, E., Spalding, M., 2002. Reefs at risk in Southeast Asia. World Resources Institute, Washington DC, USA, 72 pp.

Caddy, J.F., 1989. Marine invertebrate fisheries: their assessment and management. Wiley-Interscience, 752 pp.

Chadwick-Furman, N.E., Loya, Y., 1992. Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat. Red Sea Mar. Biol. 114, 617–623.

Chadwick-Furman, N.E., Goffredo, S., Loya, Y., 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. J. Exp. Mar. Biol. Ecol. 254, 199-218.

Chan T., Sadovy Y., 1998. Profile of the marine aquarium fish trade in Hong Kong. Aqu. Sci. and Cons. 2, 197-213.

Connell, J.H., 1973. Population ecology of reef building corals. In: Jones, O.A., Endean, R. (eds.), Biology and Geology of Coral Reefs, Vol. II, Academic Press, New York, pp. 271–324.

Connell, J.H., Hughes, T.P., Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67, 461–488.

Edinger, E.N., Jompa, J., Limmon, G.V., Widjatmoko, W., Risk, M.H., 1998. Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. Mar. Pollut. Bull. 36, 671-630.

Edmunds, P.J., Elahi, R., 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastrea annularis*. Ecol. Monogr. 77, 3-18.

Erdmann, N. 1995. The ABC guide to coral reef fisheries in Southwest Indonesia, Sulawesi. In: NAGA, the ICLARM Quaterly, 18, 4-6.

Glynn, P.W., Colley S.B., Ting, J.H., Mate J.L., Guzman, M., 2000. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama and Galapagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp. Mar. Biol. 136, 1432-1793.

Goffredo, S., Arnone, S., Zaccanti, F., 2002. Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europea* (Scleractinia, Dendrophylliidae). Mar. Ecol. Prog. Ser. 229, 83-94.

Goffredo, S., Chadwick-Furman, N.E., 2003. Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea. Mar. Biol. 142, 411-418.

Goffredo, S., Mattioli G., Zaccanti F., 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Coral Reefs 23, 433-443.

Green, E.P, Shirley, F., 1999. The global trade in corals. World Conservation Monitoring Centre. World Conservation Press, Cambridge UK, 60 pp.

Grigg, R.W., 1984. Resource management of precious corals: a review and application to shallow water reef building corals. P.S.Z.N.I. Mar. Ecol. 5, 57–74.

Gulland, J.A., 1971. The fish resources of the oceans. West fleet survey. Fishing News Ltd., FAO, 255pp.

Hamid, L.M.O., 2007. Genetic population structure of the pink anemonefish *Amphiprion perideraion* (Pomacentridae) in the Indo-Malay Archipelago. MSc Dissertation, University of Bremen.

Harriott, V.J., 2003. Can corals be harvested sustainably? Ambio 32, 130-133.

Harrison, P.L., Wallace C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (eds.), Ecosystems of the World, vol. 25, Coral reefs. Elsevier Science Publishers, Amsterdam,133-207.

Highsmith, R.C., 1982. Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7, 207-226.

Hoeksema, B.W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zool. Verhand. 254, 1-295.

Hoeksema, B.W., Moka, W., 1989. Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. Net. J. Sea. Res. 23, 149-160.

Hoeksema, B.W., 1990. Cross-shelf distribution patterns of mushroom corals (Fungiidae) in the southern Makassar Strait. In: Hoeksema (chapter 3.3) Systematics and ecology of mushroom corals (Scleractinia: Fungiidae). Ph.D. thesis, Leiden University, 361-452.

Hoeksema, B.W., 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema, W. (eds.), Biogeography, time and place: distributions, barriers and islands. Topics in Geobiology 29, 117-178.

Hopley, D., Suharsono, 2000. The Status of Coral Reefs in Eastern Indonesia. Townsville, Australia: Global Coral Reef Monitoring Network, 38 pp.

Hughes, T.P., Jackson, J.B.C., 1980. Do Corals Lie About Their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion. Science 209, 713-715.

Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55, 141–166.

Hughes, T.P., Connell, J.H., 1987. Population dynamics based on size or age? A reef-coral analysis. Am. Nat. 129, 818-829.

Hughes, T.P., Bellwood, D.R., Connnolly, S.R., 2002. Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol. Lett. 5, 773-784.

Johnson, K.G., 1992. Population dynamics of a free-living coral: recruitment, growth and survivorship of Manicina areolata (Linnaeus) on the Caribbean coast of Panama. J. Exp. Mar. Biol. Ecol. 164, 171–191.

Jones, G.P., Planes S., Thorrold S.R., 2005. Coral reef fish larvae settle close to home. Curr. Biol. 15, 1314-1318.

Jones, R., 2008. CITES, corals and customs: a review of the international trade in wild coral. In: Proceedings of the 1st International Coral Husbandry Symposium, Arnhem, Holland, in press.

Kimura, M., Weiss, G.H., 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49, 561-576.

Knittweis, L., Kraemer, W.E., Timm, J., Kochzius, M., 2008. Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. Conserv. Genet., doi: 10.1007/s10592-008-9566-5.

Lal, P., Kinch, J., 2005. Financial assessment of the marine trade of corals in the Solomon Islands. Report prepared for the Departments of Fisheries and Marine Resources, Forestry and Environment and Conservation, Ministry of Natural Resources. The Solomon Islands Government, Honiara, 32 pp.

Lilley, G., 2001. A review of Indonesian corals in the trade with reference to their trade, population status and distribution in Indonesia. Traffic Europe Report, Brussels, 18 pp.

Lourie, S.A., Green, D.M., Vincent, A.C.J., 2005. Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: Hippocampus). Mol. Ecol. 14, 1073-1094.

Lucas, J.S., 1988. Giant clams: description, distribution and life history. In: Copland, J.W., Lucas, J.S. (eds.), Giant clams in Asia and the Pacific. Aust. Cent. Int. Agric. Res. Monogr. 9, 21–32.

Magalon, H., Adjeroud, M., Veuille, M., 2005. Patterns of genetic variation do not correlate with geographical distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. Mol. Ecol. 14, 1861-1868.

Mackenzie J.B., Munday P.L., Willis, B.L., Miller D.J., Van Oppen M.J.H., 2004. Unexpected patterns of genetic structuring among locations but not colour morphs in *Acropora nasuta* (Cnidaria; Scleractinia). Mol. Ecol. 13, 9-20.

Meesters, E.H., Hilterman M., Kardinaal, E., Keetman, M., de Vries M., Bak, R.P.M., 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar. Ecol. Prog. Ser. 209, 43-54.

Miclat, E.F.B., Ingles J.A., Dumaup, J.N.B., 2006. Planning across boundaries for the conservation of the Sulu-Sulawesi marine ecoregion. Ocean Coast. Manage. 49, 597-609.

Moll, H., 1983. Zonation and diversity of Scleractinia on reefs off S.W. Sulawesi, Indonesia. Univ. Leiden Thesis, Leiden, 107 pp.

Mulliken, T.A., Nash, S.V. 1993. The recent trade in Philippine corals. TRAFFIC Bulletin 13, 97–105.

Munro, J.L., Pauly, D. 1983. A simple method for comparing the growth of fishes and invertebrates. ICLARM Fishbyte 1, 5-6.

Nelson, J.S., Hoddell, R.J., Chou, L.M., Chan, W.K., Phang, V.P.E., 2000. Phylogeographic structure of the false clownfish, *Amphiprion ocellaris*, explained by sea level changes on the Sunda Shelf. Mar. Biol. 137, 727-736.

Nishikawa, A., Katoh, M., Kazuhiko, S., 2003. Larval settlement and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Mar. Ecol. Prog. Ser. 256, 87-97.

Nozawa, J., Harrison, P.L., 2005. Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. Coral Reefs 24, 274-282.

Nuryanto, A., Kochzius, M., 2006. Limited gene flow in the giant clam *Tridacna crocea* across the Indo-Malay Archipelago. In: Abstracts of the 6th European meeting of the International Society for Reef Studies (ISRS), Bremen, Germany, 19-22 September 2006.

Oliver, K., 2003. World trade in ornamental species. In: Cato, J.C., Brown C.L. (eds.), Marine ornamental species: collection, culture and conservation. Iwoa State Press, 49-63.

Pauly, D., 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Stud. Rev. 8. 325pp.

Pet-Soede, L., Erdmann M., 1998. An overview and comparison of destructive fishing practices in Indonesia. SPC Live Reef Fish Info. Bul. 4, 28-36.

Pet-Soede, C., Van Desen W.L.T., Hiddink J.G., Kuyl S., Machiels M.A.M., 2001. Can fishermen allocate their fishing effort in space and time on the basis of their catch rates? An example from Spermonde Archipelago, S.W. Sulawesi, Indonesia. Fisheries Manag. Ecol. 8, 15-36.

Pauly, D., 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Stud. Rev. 8, 325 pp.

Raymakers, C., 2001. Review of trade in live corals from Indonesia. Traffic Europe, Brussels, 18 pp.

Raymakers, C., 2002. EU trade on stony corals from Indonesia. In: Bruckner, A.W. (ed.), Proceedings of the international workshop on the trade in stony corals: development of sustainable management guidelines. NOAA Technical Memorandum NMFS-OPR-23, Silver Spring, MD, 152 pp.

Richmond, R.H., 1989. Competency and dispersal of spawned versus brooded coral planula larvae. Paper presented at the 6th International Coral Reef Symposium, Townsville, Australia, 08-12 September 1988.

Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 pp.

Ross, M.A., 1984. A quantitative study of the stony coral fishery in Cebu, Philippines. P.S.Z.N.I. Mar. Ecol. 5, 75–91.

Reksodihardjo-Lilley, G., Lilley, R., 2007. Towards a sustainable marine aquarium trade: an Indonesian perspective. SPC Live Reef Fish Info. Bul. 17, 11-19.

Rodriguez-Lanetty, M., Hoegh-Guldberg, O., 2002. The phylogeography and connectivity of the latitudinally widespread scleractinian coral *Pleisiastrea versipora* in the Western Pacific. Mol. Ecol. 11, 1177-1189.

Sadovy, Y.J., Vincent A.C.J., 2002. Ecological issues and the trades in live reef fishes. In: Sale, P.F. (ed.), Coral reef fish dynamics and diversity in a complex ecosystem. Academic Press, San Diego, 391-420.

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bull. Int.-Am. Trop. Tuna Comm. 1, 27-56.

Soegiarto, A., Polunin, N., 1981. Marine Ecosystems of Indonesia: A Basis for Conservation. Report IUCN/WWF Indonesia Programme, Bogor, 254 pp.

Sparre, P., Venema, S.C., 1998. Introduction to tropical fish stock assessment. FAO Fisheries Technical Paper 306/1. 407pp.

Sugama, K., Haryanti, Benzie, J.A.H., Ballment E., 2002. Genetic variation and population structure of the giant tiger prawn, *Penaeus monodon*, in Indonesia. Aquaculture 205:37-48

Takabayashi, M., Hoegh-Guldberg, O., 1995. Ecological and physiological differences between two colour morphs of the coral *Pocillopora damicornis*. Mar. Biol. 123, 705-714.

Thompson, W.F., Bell F.H., 1934. Biological statistics of the Pacific halibut fishery. 2. Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. Comm. 8, 49pp.

Tomascik, T., Mah, A.J., Nontji, A., Moosa, M.K., 1997. The Ecology of the Indonesian Seas Part One. The Ecology of Indonesia Series Volume VII. Periplus, Singapore, 642 pp.

Tsounis, G., Rossi, S., Gili J.M., Arntz W., 2007. Red coral fishery at the Costa Brava (NW Mediterranean): case study of an overharvested precious coral. Ecosystems 10, 975-986.

Vollmer, S.V., Palumbi, S.R. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: Implications for the recovery of endangered reefs. J. Hered. 98, 40-50.

Von Bertalanffy, L., 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol.10, 181–213.

Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems, time durations. J. Biogeogr. 27, 1153-1167.

Wabnitz, C., Taylor, M., Green E., Razak, T., 2003. From ocean to aquarium. UNEP-WCMC, Cambridge, UK, 66 pp.

Waller, R.G., Tyler P.A., Gage J.D., 2002. Reproductive ecology of the deep-sea scleractinian coral *Fungiacynthus marenzelleri* (Vaughn, 1906) in the northeast Atlantic Ocean. Coral Reefs 21, 325-331.

Whitaker, K., 2004. Non-random mating and population genetic subdivision of two broadcasting corals at Ningaloo Reef, Western Australia. Mar. Biol. 144, 593-603.

Williams, S.T., Benzie, J.A.H., 1996. Genetic uniformity of widely separated populations on the coral reef starfish *Tinckia laevigata* from the East Indian and West Pacific Oceans, revealed by allozyme electrophoresis. Mar. Biol. 126, 99-107.

Wilson, J.R., Harrison, P.L., 1998. Settlement-competency periods of larvae of three species of scleractinian corals. Mar. Biol. 131, 339-345.

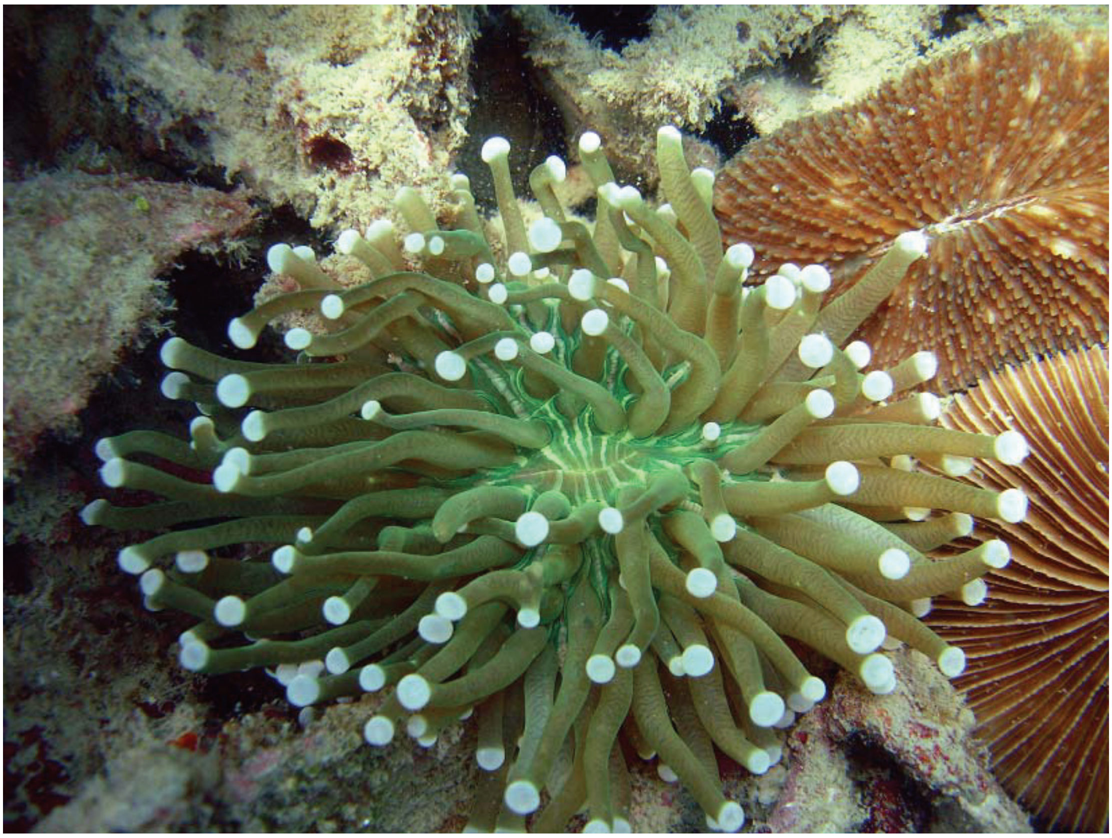
Wijesekara, R.G.S., Yakupitiyage A., 2001. Ornamental fish industry in Sri Lanka: present status and future trends. Aqu. Sci. and Cons. 3, 241-252.

Wright, S., 1943. Isolation by distance. Genetics 28, 1.

Yamashiro, H., Yamazato K., 1987. Studies on the detachment of the discs of the mushroom coral *Fungia fungites* with special reference to hard structural changes. Galaxea 6, 163-175.

Chapter 2

Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia



Heliofungia actiniformis **with tentacles fully extended**

Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia

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Abstract

The fungiid *Heliofungia actiniformis* is one of the most popular coral species in the Indonesian aquarium trade, yet information on this species' biology is limited, and existing harvest management efforts clearly lack a scientific basis. *H. actiniformis* growth rates, population size-frequency distributions and the seasonality of recruitment rates were measured at three replicate sites in the Spermonde Archipelago, South Sulawesi. Growth and population models were applied to estimate coral ages, mortality rates and the optimal harvesting size. Growth was isometric and decreased linearly with polyp size. High numbers of attached polyps budded from clusters of stalks attached to the reef, with each cluster originating from the settlement of a sexually produced larva. Neither the settlement of sexual recruits nor their asexual budding showed seasonality. The overall population structure reflected the very high mortality rates of young, attached polyps ($Z = 0.5\text{-}0.6\ yr^{-1}$), and the much lower mortalities of free-living individuals ($Z = 0.05\text{-}0.08\ yr^{-1}$). There were no statistically significant differences in (1) overall mortality rates (2) the age-frequency distributions of polyps aged 0-15 years between sites. Differences in the abundance of large *H. actiniformis* polyps at the three replicate sites could be correlated with variations in rubble cover. The application of the Beverton and Holt model revealed an optimum potential yield of *H. actiniformis* at 12 cm, corresponding to a polyp age of 20 years.

Keywords: mushroom coral; population ecology; population yield; ornamental trade; Indo-Pacific.

Introduction

Understanding the demographic patterns of scleractinian coral populations, as well as the relationship of population dynamics to environmental influences, is vital to determine the processes at work behind the global decline of coral reefs (as documented e.g by. Gardner et al. 2003; Bellwood et al. 2004; Wilkinson 2004). An estimated 11-12 million pieces of live coral are collected from reefs annually for the aquarium trade (Wabnitz et al. 2003), and potential management approaches to ensure long term trade sustainability rely on a detailed understanding of the individual species' demographic characteristics. However, the information available to date on coral population dynamics is poor and scattered (Goffredo et al. 2004), and virtually lacking for the Indo-Malay Archipelago, despite this region's importance as the world's coral biodiversity hotspot (Hughes et al. 2002) and leading role in the global coral trade (Wabnitz et al. 2003).

This lack of information is partly due to difficulties in studying population dynamics because of the slow growth and long lives of scleractinian corals, with only few authors attempting long term studies (Connell et al. 1997; Edmunds and Elahi 2007). Furthermore the interpretation of size-frequency data using standard assessment techniques is rarely possible because of the corals' colonial nature: processes such as fragmentation, fusion and partial colony mortality distort age-size relationships in the great majority of species (Hughes 1984; Babcock 1991; Goffredo et al. 2004). In combination with variable growth rates and great longevity, this may result in a wide size range within a single cohort (Hughes and Connell 1987).

This is not the case for coral species which grow in distinct forms (e.g., *Pocillopora verrucosa*, Grigg 1984; *Corallium rubrum*, Tsounis et al. 2006), or where partial colony mortality is evident and can be quantified readily (e.g., *Goniastrea aspera*, *Platygra sinensis*, Babcock 1991; *Siderastrea siderea*, Lewis 1997). Moreover, a few aclonal coral species do exist, where polyps are solitary and where size can be directly related to age if growth rate data is available. Age may be a linear function of individual length, but in coral species which grow determinately age-size relationships must be estimated using a growth curve such as the widely applied von Bertalanffy growth curve (von Bertalanffy 1938). The fungiidae for instance are a family comprising a number of conspicuous solitary species with determinate growth, which lend themselves to size- and age-based demographic assessments through the application of the von Bertalanffy growth model (e.g., *Fungia granulosa*, Chadwick-Furman et al. 2000; *Ctenactis echinata*, *Fungia scutaria*, *Fungia fungites*, *Danafungia* spp., Goffredo and Chadwick-Furman 2003).

The typical life cycle of a mushroom coral can be divided into three major life history stages, containing phases of both sexual and asexual reproduction. During the planktonic phase, the sexually produced larvae seek a suitable substratum for settlement (Abe 1937). This marks the beginning of the sessile phase, where polyps are attached to the substratum with a stalk termed anthocaulus. After a growth period, polyps detach and become free-living, marking the beginning of the anthocyathus phase, leaving behind the anthocaulus stalk which may regenerate tentacles and turn into a new polyp (Hoeksema 1989). Many species are further able to reproduce asexually via buds on the anthocyathus skeleton after polyp injury or death (Boschma 1922; Hoeksema 1989; Gilmour 2002b; Hoeksema 2004). Extracting biological information from the size frequencies of mushroom coral populations will thus require the consideration of these life-history traits.

Coral population size structures are also influenced by differences in the exposure regimes of their habitats (e.g., see Hughes 1989; Fong and Glynn 1998; Meesters et al. 2001), and in the case of mushroom corals, disturbances are likely to affect the three life history stages to varying degrees. In the only detailed study to date, the relative contributions of sexually and asexually derived polyps as well as the resulting size-frequency structures of *F. fungites* populations at a site exposed to more frequent storms and higher sedimentation rates differed markedly from those at a nearby sheltered location (Gilmour 2004). Moreover, the importance of the various life history phases in the biology of *F. fungites* was only apparent at the exposed site: asexual buds growing on parent skeletons were only present here.

Seasonal variations in the recruitment rates of sexually derived polyps and hence the abundance of young polyps also need to be considered for the correct interpretation of size-frequency distributions: a single size-frequency distribution census will only represent a snapshot in time and as such may be misleading (e.g., Babcock 1991). Inter-seasonal differences in recruitment rates differ amongst coral taxa, though the general pattern seems to be higher recruitment rates in the warmest season (Wallace 1985; Harriot 1992; Gleason 1996; Glassom et al. 2004). Published accounts of larval recruitment data for the Indo-Malay Archipelago are however rare (but see Nacua and Alino 1994; Reyes and Yap 2001; Fox 2004), and altogether lacking for the family Fungiidae.

One of the most popular scleractinian coral species in the live aquarium trade is the fungiid *Heliofungia actiniformis*, which had the second highest collection quotas in Indonesia during 1999-2006 (~400 000 exported pieces; BKSDA Makassar, personal communications).

Although to date it is impossible to keep this coral alive in an aquarium over any extended period of time (Baquero 1991; C. Delbeek, personal communications), it is popular due to its colourful tentacles which are extended both day and night (Green and Shirley 1999). To date scientific knowledge on the ecology of *H. actiniformis* is restricted to the early studies conducted in Palau on post-larval development (Abe 1937), polyp growth (Abe 1939), polyp mobility (Abe 1940), and to brief records of field observations in the Indo-Malayan Archipelago (Moll 1983; Hoeksema and Moka 1989). Given this lack of information, the existing collection quotas must be considered arbitrary values.

The objectives of this study were to characterise the life history characteristics of *H. actiniformis* and apply population models to facilitate the application of the data for harvest management purposes. The specific goals were to (1) measure growth of *H. actiniformis* in the field and determine the von Bertalaffy growth parameters, (2) determine its population structure and important life history phases, (3) estimate the mortality rates of the different life history phases, (4) assess the seasonality of recruitment rates, and (5) estimate the optimal harvest size and age by applying a yield per recruit model.

Materials and methods

Study area

The Spermonde Archipelago in South Sulawesi extends approximately 60 km offshore and consists of about 150 islands with fringing reefs, as well as a large number of barrier and submerged patch reefs (Tomascik et al. 1997) that have supported intensive fishing activity since at least the 14th century (Erdmann 1995). Today the archipelago provides livelihoods to thousands of fisher households scattered over the islands (Pet-Soede et al. 2001), and supports one of largest live coral fisheries in Indonesia (Raymakers 2001). Reef degradation is widespread, with causes including industrial and sewage pollution from nearby Makassar, extensive bomb fishing, anchor damage and over-harvesting of coral reef resources (Edinger et al. 1998).

Moll (1983) identified a number of ecological reef zones based on shelf bathymetry and the distribution of coral species, ranging from zone one located closest to the shore, to the shelf rim adjacent to zone four, where the bottom drops almost vertically to depths of over 800m (de Klerk 1983). A detailed survey of fungiid corals in the Spermonde Archipelago confirmed that fungiid species composition is also related to these shelf zones (Hoeksema 1989). The present study was carried out at three representative reefs of zone two, where fishing for the live coral trade does not usually take place (Knittweis 2008): Bone Baku (BA), Samalona (SA) and Barrang Lompo (BL) (Fig. 1). It was deemed necessary to survey *H. actiniformis* at three replicate sites due to the very patchy nature of reefs in the archipelago, with small-scale local differences in coral rubble presumably resulting in variable levels of habitat stability and thus exposure to mechanical disturbances despite the otherwise similar habitats and environmental influences.

The region has monsoonal weather with two major seasons, the wet north-western monsoon and dry south-eastern monsoon, which extend from June-September and December-March respectively (Tomascik et al. 1997). The north-western sides of the chosen reefs, which are exposed to the stronger hydrodynamic regimes of the rainy season, were surveyed since Hoeksema (1989) found the highest mushroom coral densities in his northern/western transects.

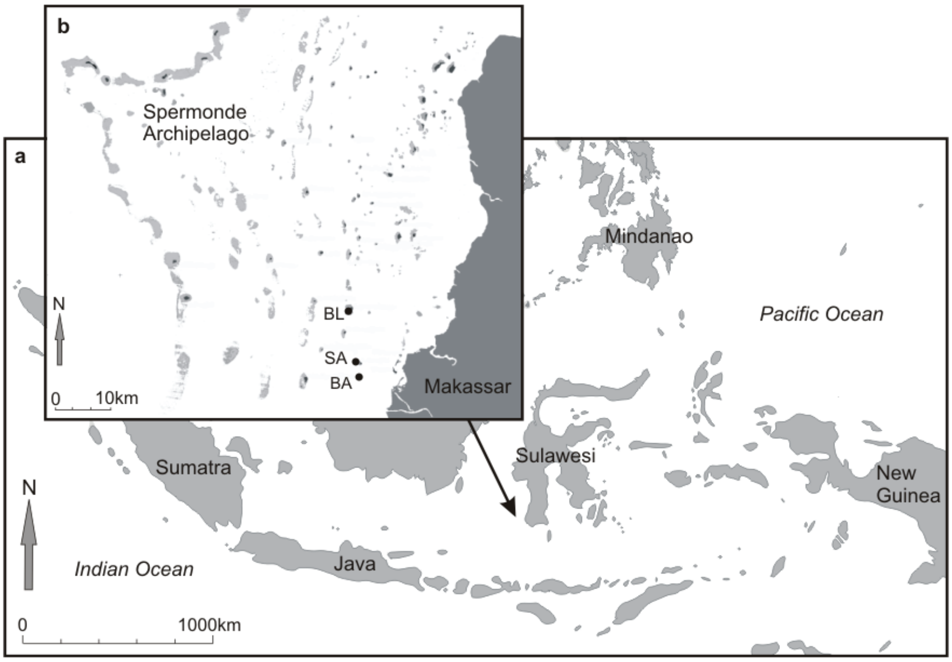

Fig. 1 a Location of Spermonde Archipelago within the Indo-Malay Archipelago **b** Sampling sites in the Spermonde Archipelago. BA: Bone Baku; SA: Samalona; BL: Barrang Lompo (taken from Landsat ETM+ satellite image, acquisition year 2002)

Polyp growth

The growth of 82 polyps was measured in Barrang Lompo at 10-12m depth from June 2005 to December 2006. Measurements covered the entire size range from 3 to 181 mm length, including attached polyps. Corals were stained in situ using the alizarin dye technique (Lamberts 1978). At the end of the growth interval stained corals were collected, tissue removed with a brush, and growth after staining measured *in situ*. For those polyps where only very little growth had taken place, small fragments of skeleton were removed at the polyp edge, and measured in the laboratory. All measurements were done by the same observer using calipers at 6 equally spaced points around the polyp perimeter.

To establish the relationships between polyp length, width and skeletal mass, 85 detached, solitary polyps from reef slopes around Barrang Lompo were collected in July/August 2005, cleaned of any visible sediment or epibiota, measured and weighed using the buoyant weight technique (after Jokiel et al. 1978) before being replaced. 72 attached polyps were additionally measured *in situ* to establish the relationship between polyp length and width for the smaller size classes.

Growth was expressed according to the von Bertalanffy growth model $L_t = L_\infty (1-e^{-kt})$, where L_t = polyp length at age t, L_∞ = asymptotic length, k = annual growth rate constant, and t = polyp age in years (von Bertalanffy 1938). A Gulland and Holt plot was used to visualize all growth data and to show growth increments as related to mean size during the growth interval. For the calculation of the growth parameters k and L_∞, a Munro Plot was used. The asymptotic length was computed by repeating the corresponding calculations of k for each individual until the coefficient of variation between the single k-values was lowest (Munro 1982). The nine largest polyps were excluded from the calculations to avoid a disproportionate influence on k by polyps approaching L_∞. A growth performance index (Φ) was calculated to compare the results of the present study with those of other mushroom coral species obtained by previous authors. The index was computed as $\Phi = 2\log L_\infty + \log k$ (Munro and Pauly 1983).

Population size and age structure

In April/May 2005 *H. actiniformis* size-frequency distributions were obtained from belt transects 150 m long and 6 m wide set up parallel to the shore. Since an initial pilot survey revealed spatially clustered populations of *H. actiniformis*, transects were only set after encountering a minimum of 5 polyps within a 3 by 6 m area. Two transect lines were set at each site, one at 8 and one at 12 m, effectively sampling a depth range of 7-15m depending on reef-slope inclination, which is where *H. actiniformis* populations were concentrated. Within each transect, all *H. actiniformis* polyps were examined and their length (along the mouth axis, after Abe 1940) as well as life cycle stage recorded as (1) attached polyp on reef anthocaulus (2) attached polyp budding on adult polyp or (3) detached anthocyathus. In addition, transects were divided into 30 plots measuring 5 by 6 m, in which the presence/absence of coral rubble and sandy patches with rubble pieces was recorded.

For the purpose of data analysis, data from 8 and 12 m were combined at each site and size-frequency distributions per 500 m^2 subsequently calculated. The age-length relationship obtained from growth measurements at Barrang Lompo was used to convert size-frequency data to age-frequency distributions at all sites. It was assumed that polyp growth rates were alike at all three study sites due to their geographic proximity. Mean ages, as well as the amount of variation in polyp sizes (coefficient of variation, CV) of the distributions were calculated as proxies for possible differences in disturbance regimes. The shapes of the age-frequency distributions were statistically compared between populations censused at Bone Baku, Samalona and Barrang Lompo using a two-sample Kolmogorov-Smirnov (KS) test (Adjeroud et al. 2007), and a Bonferroni correction was applied to adjust for multiple comparisons (i.e., $p = 0.017$ was used for each comparison to obtain an overall α of 0.05).

Total mortality rates (Z) were calculated separately for the attached and free-living life cycle phases by applying a length-converted catch curve analysis (Pauly 1984). The midpoint of each length class was converted to an age class using the inverse von Bertalanffy equation relating length to age, using $t_L = -1/k * \ln(1-L/L_\infty)$. The time interval ($\Delta t$) from one length to the next was obtained using the equation $\Delta t = 1/k * \ln((L_\infty-L_1)/(L_\infty-L_2))$. The $\ln[C(L1,L2)/\Delta t]$ was then plotted against age for the catch curve regression analysis (after Sparre and Venema 1998). Polyps sized 0-4 and 4-15 cm in length were analysed separately. Individuals exceeding 15 cm in length were excluded from the analysis to eliminate inaccuracies in the relationship of length and age resulting from the extremely slow growth of larger polyps (after Sparre and Venema 1998). The significance of the differences between sample regression coefficients was tested by two-tailed student's t-tests, again using the Bonferroni correction to adjust for multiple comparisons.

Recruitment seasonality

To examine the influence of seasonality on the size-frequency distribution of young recruits, all polyps sized 0-4 cm within the belt transects were re-counted in October 2005, April 2006 and October 2006. Potential variations in total numbers of young polyps from sexual recruitment as well as asexual budding were thus monitored after both dry and rainy seasons. Size-frequency data was analysed by a 3-way ANOVA (factor1: size, with four levels (size classes); factor 2: season, with two levels (wet and dry); factor 3: year, with two levels (2005 and 2006).
All anthocauli found in April/October 2005 were marked and the location of newly settled sexual recruits was recorded in April as well as October 2006. Potential seasonal differences in settlement rates of sexual recruits were tested using a two-tailed student's t-test.

Cohort biomass and potential yield

H. actiniformis populations were described by the application of a modified version of the Beverton and Holt (1957) yield per recruit model, which allowed us to estimate the age at maximum production of a year class, and thus the optimal size and age for harvest. For this purpose an age-specific cohort biomass curve was generated using the polyp growth curve, the relationship between polyp skeletal mass and length, and the average of the natural mortality rates calculated above (after Grigg 1984; Chadwick-Furman et al. 2000; Tsounis et al. 2007).

Results

Polyp growth

The growth rate of coral polyps declined linearly with length (Fig. 2a), from 11.5 ± 3.6 mm yr^{-1} (mean ± SD) for the 15 smallest corals monitored (3-39 mm in length at the start of measurements), which were still in the attached life-cycle phase, to 1.0 ± 1.1 mm yr^{-1} (mean ± SD) for the 15 largest corals monitored (132-181 mm in length at the start of measurements). The growth rate over the entire size range of corals investigated was 5.7 ± 4.5 mm yr^{-1} (mean

± SD). The Munro Plot revealed a minimum coefficient of variation for the growth constant (k) = 0.0741 and the maximum expected polyp length (L_∞) = 163 mm (Fig. 2b). The value of the growth performance index (Φ') was 3.29.

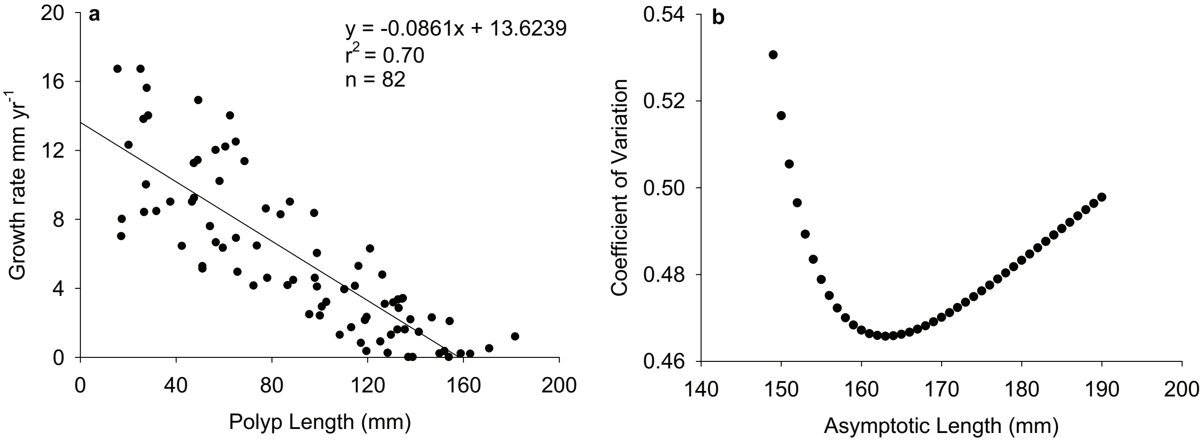

Fig. 2 a Gulland and Holt-Plot showing the linear decline in growth of *Heliofungia actiniformis* polyps with size; polyp length refers to the length attained at the mid-point between measurements. **b** Coefficient of variation around average growth rate (k) for a series of asymptotic lengths (L_∞)

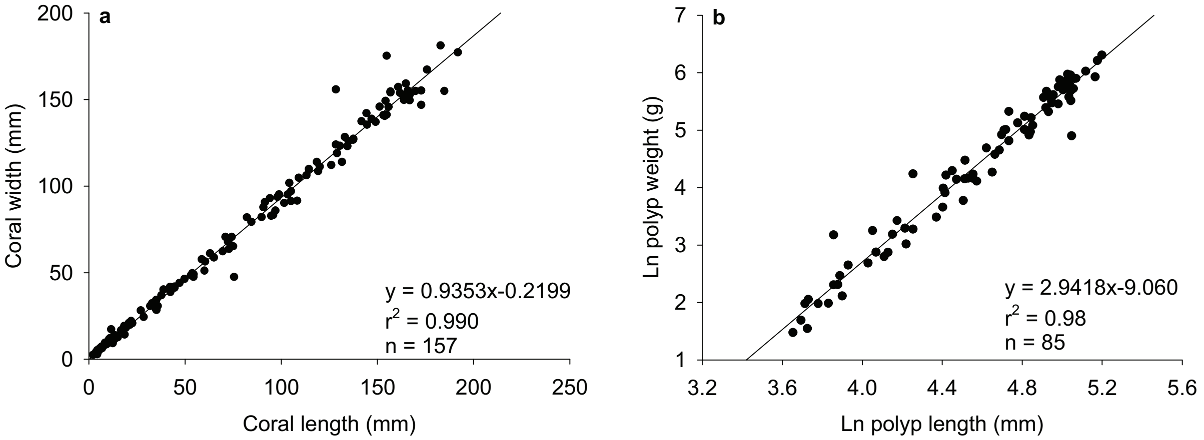

Fig. 3 a Relationship between polyp width and polyp length **b** Relationship between polyp weight and polyp length

During the lifespan of *H. actiniformis* width varied linearly with length (Fig. 3a), i.e. polyp shape did not change over time and growth was isometric. Polyp buoyant weight increased exponentially with length, and after ln-transforming the data (Fig. 3b), the equation $W = a*L^b$ could be used to calculate polyp biomass in subsequent analyses, where W was the coral body weight, L the coral length, b the slope of the regression (i.e. the exponent of the length-weight relationship) and a the x-axis intercept (after Sparre and Venema 1998).

Population size and age structure

The three study sites differed in levels of habitat rubble cover, with the highest differences apparent between Samalona and Bone Baku (Fig. 4). At Bone Baku 33% of reef segments contained rubble, 23% had sandy patches with only a limited number of rubble pieces and 43% contained no rubble at all. In contrast, 97% of reef segments in Samalona contained rubble.

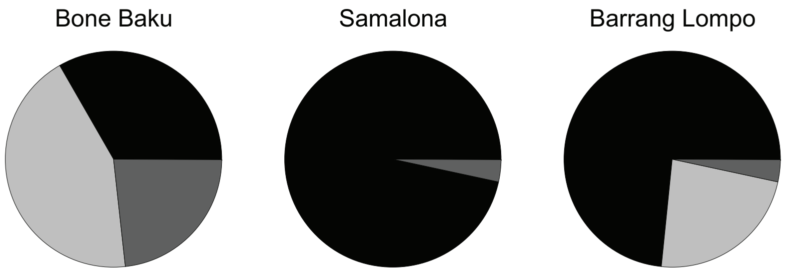

Fig. 4 Reef condition at study sites: percentage of reef segments which contained rubble (black), sandy patches with a limited number of rubble pieces (light grey) and no rubble at all (dark grey)

Overall, 74 ± 7 polyps (mean ± SD) per 500m^2 were measured, with 42 ± 6% (mean ± SD) of polyps in the attached life cycle phase. Age-frequency distributions reflected this dominance of young individuals, with 39%, 45% and 52% of polyps belonging to the 0-4 year age class intervals in Bone Baku, Samalona and Barrang Lompo respectively (Fig. 5). Mean polyp age was highest at Bone Baku (12.6 yrs), noticeably less at both Samalona (9.22 yrs) and lowest at Barrang Lompo (8.28 yrs). Conversely, the CV was lowest at Bone Baku (1.08) and highest at Barrang Lompo (1.17), with Samalona again in between the two (1.11).

The two-sample Kolmogorov-Smirnov test showed significant differences between the shapes of the age-frequency distributions found at Bone Baku/Samalona, and at Bone Baku/Barrang Lompo but not between Samalona/Barrang Lompo (BA/SA KS = 0.007, BA/BL KS = 0.0004, BL/SA KS = 0.23; $p_{crit} = 0.017$). When repeated for young polyps aged 0-15 years only, no significant differences were found (BA/SA KS = 0.16, BA/BL KS = 0.38, BL/SA KS = 0.84; $p_{crit} = 0.017$).

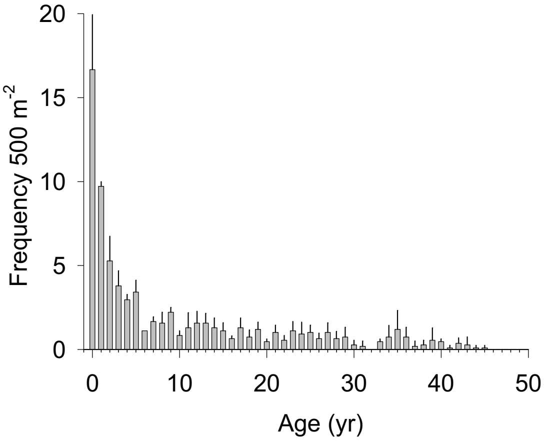

Fig. 5 Average *Heliofungia actiniformis* age-frequency distribution ± standard deviation in Spermonde (Bone Baku n = 331, Samalona n = 242, Barrang Lompo n = 281)

Only one adult polyp with asexual buds growing from the underside of the skeleton (n = 9) was found at Bone Baku. All other *H. actiniformis* polyps ≤ 3 cm in length measured over the course of this study were found either growing on anthocaulus stalks attached to the reef (97.9%), or in the immediate vicinity of such a stalk if detached prematurely.

Anthocauli grew in clusters, with 6.5 ± 3.6, 5.0 ± 4.1 and 4.8 ± 5.6 (mean ± SD) stalks branching out from a single sexual recruit at Bone Baku, Samalona and Barrang Lompo respectively. The maximum number of anthocauli found in a cluster was 46, recorded at 8 m depth at Barrang Lompo in October 2005. During the initial transect surveys, 98.3% of polyps sized ≥ 4 cm had detached and were free living; the biggest attached polyp measured in the field was 7.5 cm long and was found at Bone Baku. The smallest detached polyps measured 2.9, 0.9 and 2.6 cm at Bone Baku, Samalona and Barrang Lompo respectively.

The steeper slopes of the catch curves for polyps 0-4 cm in length illustrate the higher mortality rates of the young, attached *H. actiniformis* compared to those of detached polyps (Fig. 6). The regression analyses showed high r^2 values (0.81-0.97) except for polyps 4-15 cm long at Bone Baku, where less polyps sized 11-13 cm and more polyps sized 13-15 cm than expected with a constant mortality rate were found ($r^2 = 0.57$).

The comparison of slopes for polyps sized 0-4 cm between Bone Baku/Barrang Lompo, Bone Baku/Samalona and Barrang Lompo/Samalona showed no significant differences (t = 1.34, 0.02, 1.15 respectively, $t_{crit} = 3.94$). Similarly, the comparison of slopes for polyps sized 4-15 cm between Bone Baku/Barrang Lompo, Bone Baku/Samalona and Barrang

Lompo/Samalona revealed no significant differences (t = 1.77, 1.48, 0.67 respectively, t_{crit} = 2.63).

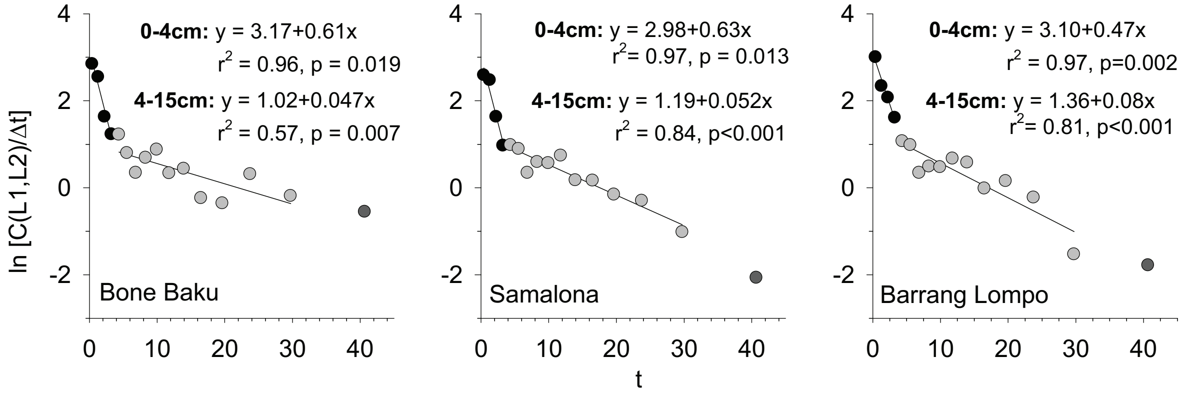

Fig. 6 Linearized catch curves based on length composition data for *Heliofungia actiniformis*. 0-4 cm: black circles, 4-15 cm: light grey circles, 16 cm: dark grey circles

Recruitment seasonality

Repeated counting of polyps measuring 0-4 cm in length on permanent transects (Fig. 7) revealed no significant differences in size frequency distributions between wet and dry seasons, and no significant differences between wet seasons in 2005/2006 and dry seasons in 2005/2006 (data was transformed by ln(x); $F_{1,32} = 0.21$, p = 0.646 and $F_{1,32} = 4.08$, p = 0.052).

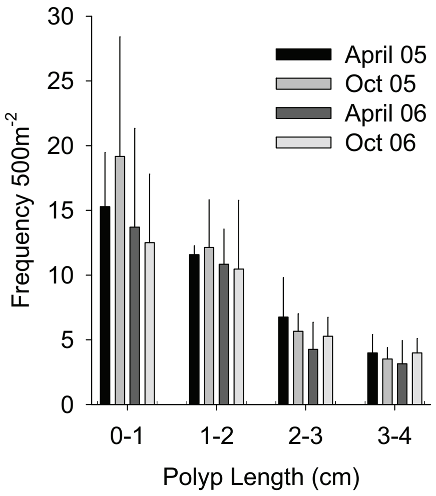

Fig. 7 Variations in size-frequency distributions of polyps 0-4 cm in length at permanent transects. Average frequencies ± standard deviations of Bone Baku, Samalona and Barrang Lompo populations

The appearance of new sexual recruits was also without seasonal pattern ($t = 0.237$, $t_{crit} = 2.78$) and infrequent, with 83% of new polyps recorded in April and October 2006 being new asexual buds.

Cohort biomass and potential yield

The biomass curve calculated for *H. actiniformis* showed a rapid increase for young polyps, before reaching the maximum of 6.54 g at an age of 20 years and a corresponding length of 12.6 cm (Fig. 8).

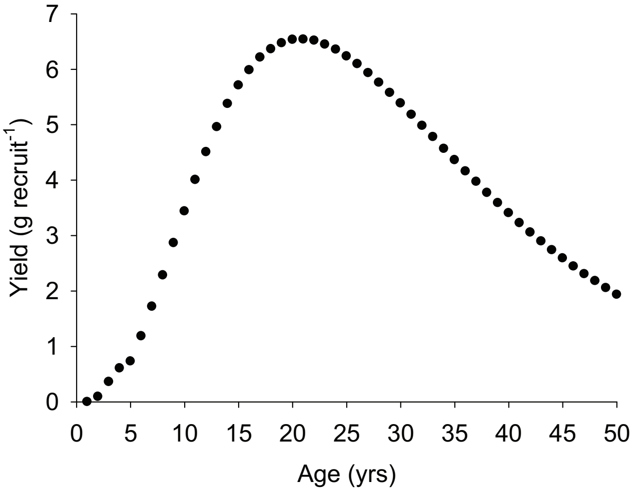

Fig. 8 Biomass per recruit curve for *Heliofungia actiniformis*

Discussion

Polyp growth

The majority of coral species are known to grow indeterminately and thus theoretically have unlimited size (Bak and Meesters 1998). Previous studies have however shown growth rates to be determinate in the detached life-cycle phase of a number of mushroom coral species: in *F. granulosa* (Chadwick-Furman et al. 2000), *C. echinata*, *F. scutaria*, *F. fungites* and *Fungia (Danafungia) spp.* (Goffredo and Chadwick-Furman 2003) growth rates decreased as coral size increased.

The Gulland and Holt Plot showed a high variability in the growth rates of the individual *H. actiniformis* polyps investigated in this study, as evidenced by the large degree of scatter around the line of best fit (Fig. 2a). However, a linear relationship between growth rates and polyp length was found, indicating non-seasonal von Bertalanffy type growth. Moreover, the assessment of coral shape parameters revealed that the width:length ratio did not change as individuals aged and growth in mass was thus isometric. Similar growth patterns have been recorded for *F. fungites*, *F. granulosa* and *Danafungia* spp. (Goffredo and Chadwick-Furman 2003). In contrast, the solitary polyps of *Fungia paumotensis* (Bablet 1985) and *F. scutaria* (Goffredo and Chadwick-Furman 2003) elongate as they grow.

The von Bertalanffy growth function has proven a useful model in the study of a number of invertebrate species with isometric growth where growth declined with size/age (Brey et al. 1990; Plaut and Fishelson 1991; Clasing et al. 1994), and indeed has been applied to a number of solitary scleractinian coral species (Bablet 1985; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004). The asymptotic individual length predicted by the application of a Munro Plot ($L_\infty = 163$ mm) was in fact considerably smaller than the maximum size measured in the field ($L = 185$ mm) and the longest *H. actiniformis* measured by Abe (1940) in Palau ($L = 195$ mm). The size frequency data collected in the course of this study and the work of Abe (1937, 1939, 1940) however confirmed the rarity of such large polyps; the model is thus considered to be representative of the overall population. Furthermore, the growth constant calculated in the present study ($k = 0.0741$) is similar to that estimated by Abe in Palau ($k = 0.0839$) and within the range of constants available in the published literature for the anthocyathi of other mushroom coral species (reviewed in Chadwick-Furman et al. 2000). Similarly, the value of the growth performance index ($\Phi' = 3.29$) was well within index values estimated for mushroom corals in previous studies (Table 1) ranging from 2.11 for *Diasteris distorta* (Yamashiro and Nishihira 1998) to 4.05 for *C. echinata* (Goffredo 1995 in Chadwick-Furman et al. 2000).

Existing variations in growth constants determined for mushroom corals have in the past been attributed to a negative relationship between growth rate and latitude (Goffredo and Chadwick-Furman 2003). The consideration of growth performance indices, i.e. how fast a polyp will attain its eventual body size, however does not seem to support this observation (Table 1). Moreover, in *F. fungites*, the only species for which data from several latitudes is available to date, a high Φ value for Eilat (3.5) contrasts a low Φ value for Sharm el Sheik (3.0), despite the relative similarity in estimated growth constants (0.049/0.088 respectively) when compared to the growth constant measured at the Great Barrier Reef (0.215). This is due to the large difference in estimated maximum length at the two sites (250 mm/107 mm), an observation which, considering the geographic proximity of the two locations, requires further study. With respect to *H. actiniformis,* the growth parameters estimated in the present study gave a lower Φ value then those calculated from the data available for Palau (3.3 and 3.5 respectively), a pattern which may be due to the fact that growth was studied at 10-12 m and 0-2 m depth respectively. Indeed, although declining growth rates with depth have been shown for scleractinian coral species in the past (e.g., see Huston 1985; Boscher and Meesters 1992; Miller 1995), this parameter has received little attention in existing studies of mushroom coral population dynamics.

Table 1 Growth parameter values in different species of mushroom coral

Species	**Location**	**Depth (m)**	**L_∞ (mm)**	**k**	**Φ'**	**Reference**
Ctenactis echinata	Sharm el Sheik, Egypt	6-12	323	0.109	4.05	Goffredo 1995[a]
Ctenactis echinata	Eilat, Israel	2-40	428	0.053	3.99	Goffredo & Chadwick-Furman 2003
Fungia paumotensis	Mururoa, Tahiti	10	147	0.404	3.94	Bablet, 1985
Fungia scutaria	Eilat, Israel	2-40	248	0.068	3.62	Goffredo & Chadwick-Furman 2003
Fungia fungites	Great Barrier Reef, Australia	0-3	133	0.215	3.58	Stephenson & Stephenson 1933[a]
Heliofungia actiniformis	Palau, Micronesia	0-2	195	0.084	3.50	Abe 1940
Fungia fungites	Eilat, Israel	2-40	250	0.049	3.49	Goffredo & Chadwick-Furman 2003
Danafungia spp.	Eilat, Israel	2-40	227	0.054	3.44	Goffredo & Chadwick-Furman 2003
Heliofungia actiniformis	**Sulawesi, Indonesia**	**10-12**	**163**	**0.074**	**3.29**	**Present Study**
Fungia granulosa	Eilat, Israel	6	118	0.110	3.18	Chadwick-Furman et al. 2000
Fungia fungites	Sharm el Sheik, Egypt	6-11	107	0.088	3.00	Goffredo 1995[a]
Diasteris distorta	Okinawa, Japan	-	19	0.360	2.11	Yamashiro & Nishihira 1998

[a] referenced in: Chadwick-Furman et al. 2000

Population size and age structure

The average number of *H. actiniformis* polyps surveyed per transect was similar to that encountered by Hoeksema in 1989 (7 and 9 polyps per 50m^2 respectively). Possible explanations for the small decline in polyp numbers may be (1) the overall decline in reef health in the Spermonde Archipelago over the past decades, (2) occasional harvesting, although fishermen negated targeting the sites investigated in this study, and actively harvested sites have much lower numbers of *H. actiniformis* (Knittweis 2008) and (3) the different survey techniques used, which in fact make detailed comparisons tenuous.

A dominance of small colonies and of only few specimens surviving to large sizes has been shown for a number of apparently healthy scleractinian coral populations (Hughes and Jackson 1985; Lewis 1989; Babcock 1991; Vermeij and Bak 2002; Adjeroud et al. 2007). In previous studies of mushroom corals, a high abundance of attached polyps and subsequent exponential decrease in the frequency of individuals with age was inferred for *F. granulosa* (Chadwick-Furman et al. 2000), *C. echinata*, *F. fungites* and *Danafungia* spp. (Goffredo and Chadwick-Furman 2003), although only a limited number of attached polyps were actually found and measured. Focusing on young attached polyps in the present study confirms that in populations of *H. actiniformis* the age structure is indeed characterised by a marked decrease in frequency of individuals with age. However, the results did not show a uniform exponential decline in numbers, but rather indicated a pronounced effect of the different life cycle stages on the overall population structure, with high mortality rates for attached polyps ($Z = 0.47$-0.63) and much lower ones for detached polyps ($Z = 0.047$-0.080). The 42% of surveyed polyps in the attached life cycle stage are contrasted by only 23% observed by Hoeksema (1989), but again variable surveying techniques make comparisons tenuous. The 23% given by Hoeksema is an average taken over all four reef zones of the Archipelago, yet it is likely that recruit numbers are higher in zones two and three, which are the preferred habitats of *H. actiniformis* (Hoeksema 1989). Whilst Hoeksema surveyed all mushroom species in his transects, the present study focused on attached *H. actiniformis* stages, with observers repeatedly searching all nooks and crannies for hidden polyps.

Even though the differences in mortality rates of both attached and detached polyps were not significant between sites, only few polyps survived to an estimated age of 40 years at Samalona and Barrang Lompo, compared to Bone Baku, where a noteworthy number of old polyps was found. This difference was reflected in the significantly different shapes of the age-frequency distributions, as well as the higher mean age and its lower coefficient of variation at Bone Baku when compared to Samalona and Barrang Lompo. Since all sites were located close to one another and exposed to similar environmental influences, the higher prevalence of coral rubble at Barrang Lompo and Samalona (Fig. 4) is the most likely explanation. Interestingly, the unstable nature of coral rubble as a substrate seems to have primarily impacted the survival rates of the largest polyps, since there was no longer a statistically significant difference when the shapes of the 0-15 year old polyps' age-frequency distributions were compared. A possible explanation may be that whilst *H. actiniformis* polyps of 6-10 cm are able to inflate their tissue and overturn to a normal position when turned upside down (Abe 1939), larger polyps may be unable to do so due to the exponential increase in skeletal weight with polyp length (Fig. 3b). Older polyps may thus be more vulnerable to become buried and killed by rubble avalanches generated during storms (Hoeksema 1989).

Asexual budding has been proposed as a mechanism enabling fungiid populations to recover and recolonise sites following disturbances (Krupp et al. 1992). Indeed, a recent study of *F. fungites* populations revealed that the importance of asexual budding from parent polyps as opposed to budding from sexually recruited reef stalks depended on the level of disturbance. At an exposed site, a large number of parent skeletons with attached buds were found, whereas at a sheltered site only reef stalks were encountered (Gilmour 2004). Even though the study sites experience severe wave action during the north-west monsoon, only 2.5% of the attached polyps found during the transect surveys were found growing on a single live adult polyp at Bone Baku. Boschma (1922) observed similar buds on the undersides of live polyps during an expedition in Java, Indonesia, but concluded them to be an 'abnormal phenomenon'. Moreover, mechanical disturbance as a result of shifting rubble pieces would have been higher at Samalona and Barrang Lompo when compared to Bone Baku, yet no polyps attached to a parent polyp were recorded at these sites. As the ability to grow asexual buds on parent skeletons was not observed at any of the sites, it may be concluded that *H. actiniformis* may be less resilient to disturbances compared to other fungiid species.

By contrast, the repeated production of anthocaulus stalks from a single sexual recruit was the main mode of asexual reproduction in the present study. Such prolific budding by reef stalks seems to be unique to *H. actiniformis* as the sexual recruits of other mushroom corals only produce a single stalk which may occasionally regenerate tentacles (Chadwick-Furman and Loya 1992; Gilmour 2004). The existence of clustered anthocaulus stalks in *H. actiniformis* was first described by Boschma (1922), Abe (1937) and Hoeksema (1989), but details of their dynamics and thus their importance in this species life cycle was hitherto unknown.

However, the high natural mortality rates of the attached polyps measured in the field limited the contribution of these asexual recruits to the population beyond the initial stage of bud production. Similarly, no detached polyps with a common genotype were found despite prolific asexual budding on parent skeletons of *F. fungites* at a site in the Dampier Archipelago, Australia (Gilmour 2002a). Whilst chronic sedimentation seemed responsible for the high mortality rates of the small polyps in the Dampier Archipelago, competition by other sessile macro-organisms (e.g., Chadwick-Furman and Loya 1992; McCook et al. 2001) as well as predation by corallivorous fish and gastropods (e.g. Bak and Engel 1979) are frequently responsible for the limited survival of young coral recruits. It is likely that sedimentation from the plume of the rivers Jene Berang and Maros as well as competition by increasingly prolific algal growth on the nearshore reefs of the Spermonde Archipelago and predation all interacted to cause the high mortality rates observed during the course of this study. The potentially lower level of physical disturbance due to lower rubble levels at Bone Baku did not significantly reduce the mortality rates of attached polyps, although a higher average number of buds per cluster as well as a larger size at first detachment were noted at this site. Similarly, sexual recruits detached later and were thus of a larger size at a site sheltered from physical disturbances in Australia (Gilmour 2004). Attached polyps were primarily observed well hidden in cryptic habitats, frequently under small ledges and overhangs. Once settled in such a favorable micro-habitat, successful larvae could bud a high number of stalks and thus produce a large number of small polyps, which may explain why the presence of rubble was less detrimental to recruitment in this species compared to other scleractinian corals (Fox 2004).

Recruitment seasonality

There was no correlation between the strength of 0-4 cm size classes and sampling season. A single population census, albeit but a snapshot in time, thus gave an accurate representation of population structure in this species during the investigated period. The size frequency distributions monitored from April 2005 till October 2006 reflected the dynamics of both asexual reproduction by budding anthocaulus stalks and sexual reproduction by the settlement of planktonic larvae. The monitoring of sexual recruits over the rainy season in October 2005-April 2006 and the subsequent dry season in April 2006-October 2006 did not reveal any patterns of seasonality either, with only a very limited number of sexual recruits recorded at all sites over both sample intervals. Asexual recruitment was thus the primary mode of reproduction observed during the study period.

The three surveyed sites were used as replicate samples in analyses, and it was thus assumed there were no site-specific effects on recruitment rates. This assumption was deemed plausible since an investigation into the population genetics of *H. actiniformis* in the Spermonde Archipelago revealed a lack of genetic structuring between Samalona and Barrang

Lompo, i.e. panmixia of planktonic larvae (Knittweis et al. 2008). Moreover, the swimming period of *H. actiniformis* larvae has been estimated at 2 to 3 days (Abe 1937), sufficient time for dispersal, especially if the larvae are caught in currents. A study of *H. actiniformis* reproduction, recruitment on settlement tiles and early growth is needed to rule out the remaining possibility that high mortality rates in the period between initial settlement and the point when the coral spat reached a size large enough to be detected in the field masked settlement seasonality in sexual recruits.

Cohort biomass and potential yield

The Beverton and Holt model was used to estimate the age at which *H. actiniformis* attained maximum population biomass levels and thus to calculate optimum harvest sizes. The model has been applied to coral species repeatedly in both tropical and temperate ecosystems (Table 1), and has been hailed as a solution to the current shortcomings in the management of exploited coral populations (Chadwick-Furman et al. 2000; Goffredo et al. 2004). While it has been successfully used to manage the harvest of the black coral in Hawaii (Grigg 2001), and to advise the management of red coral harvesting in Spain (Tsounis et al. 2007), an application to a species exploited for the live coral aquarium trade has to date not been attempted.

According to the present estimates, the minimum harvest age for *H. actiniformis* by the aquarium trade in the Spermonde Archipelago should be 20 years, corresponding to a size of about 12-13 cm. Due to the low natural mortality rates of detached polyps, *H. actiniformis* reached the point of maximum yield/recruit significantly later than related mushroom coral species (5-14 years, Table 2), thus making it more vulnerable to overexploitation.

Abe (1937) observed spawning in *H. actiniformis* polyps measuring 8 cm in length, but not in those measuring 7 cm. Taking this estimate as the size at first reproduction, a size limit of 12 - 13 cm would thus also ensure a sufficient buffer period for sexual reproduction and ensure a continuous supply of larvae. This would sustain the population in the long-term, and fulfill one of the major assumptions of the Beverton and Holt model, that harvest does not affect recruitment.

Another assumption underlying the application of this model is that the population investigated is in a steady state, which implies that none of the age classes should be over- or under-represented. As discussed above, an apparent under-representation of polyps aged 30-45 years was however noted at Barrang Lompo and Samalona. It follows that (1) while the present study gives an accurate description of present day *H. actiniformis* demographic traits in the Spermonde Archipelago as evidenced by the replicability of the findings regarding natural mortality rates of both attached and detached polyps, the results obtained need to be interpreted with caution and (2) the conclusions of this study may only hold as long as reefs are not degraded further, which would expose polyps to even higher rubble cover and hence even more unstable reef slopes.

Table 2 Ages at the attainment of maximum biomass/recruit known for anthozoans

Reference	**Species**	**Location**	**Age (yrs)**
Goffredo & Chadwick-Furman 2003	*Fungia scutaria*	Eilat, Israel	5
Goffredo et al. 2004	*Balanophyllia europea*	Calafurnia, Italy	6
Grigg 1984; Ross 1984	*Pocillopora verrucosa*	Cebu, Philippines	6
Goffredo & Chadwick-Furman 2003	*Fungia fungites*	Eilat, Israel	8
Chadwick-Furman et al. 2000	*Fungia granulosa*	Eilat, Israel	9
Goffredo & Chadwick-Furman 2003	*Danafungia spp.*	Eilat, Israel	10
Goffredo & Chadwick-Furman 2003	*Ctenactis echinata*	Eilat, Israel	14
Present study	***Heliofungia actiniformis***	**Sulawesi, Indonesia**	**20**
Grigg, 1976	*Anthipathes dichotoma*	Hawaii	28
Grigg, 1976	*Corallium secundum*	Hawaii	34
Tsounis et al. 2007	*Corallium rubrum*	Cap de Creus, Spain	98

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References

Abe N (1937) Post-larval development of the coral *Fungia actiniformis* var. palawensis Doederlein. Palao Trop Biol Stn Stud 1:73-93

Abe N (1939) Migration and righting reaction of the coral*, Fungia actiniformis* var. palawensis Doederlein. Palao Trop Biol Stn Stud 4:671-694

Abe N (1940) Growth of *Fungia actiniformis* var. palawensis Doederlein and its environmental conditions. Palao Trop Biol Stn Stud 5:105-145

Adjeroud M, Pratchett MS, Kospartov MC, Lejeusne C, Penin L (2007) Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. Hydrobiologia 589:117-126

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol Monogr 61:225–244

Bablet JP (1985) Report on the growth of a scleractinia (*Fungia paumotensis*). Proc 5th Int Coral Reef Symp 4:361-365

Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54:341-352

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size frequency distributions. Mar Ecol Prog Ser 162:301–306

Baquero J (1991) Scleractinians or stony corals and the aquarium trade. Part I. Sea Wind 5:6-12

Bellwood DR, Hughes TP, Folke C, Nystroem M (2004) Confronting the coral reef crisis. Nature 429:827-833

Beverton RJH, Holt SV (1957) On the dynamics of exploited fish populations. London: Chapman and Hall

Boschma H (1922) On budding and coalescence of buds in *Fungia fungites* and *Fungia actiniformis*. Proc Kon Ned Akad Wet 24:257-268

Boscher H, Meesters EH (1992) Depth related changes in the growth rate of *Montastrea annularis*. Proc 7th Int Coral Reef Symp 1:507-512.

Brey T, Arntz WE, Pauly D, Rumohr H (1990) *Arctica* (*Cyprina*) *islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. J Exp Mar Biol Ecol 136:217-235

Chadwick-Furman NE, Loya Y (1992) Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. Mar Biol 114:617–623

Chadwick-Furman NE, Goffredo S, Loya Y (2000) Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. J Exp Mar Biol Ecol 254:199-218

Clasing E, Brey T, Stead R, Navarro J, Asencio G (1994) Population dynamics of *Venus antiqua* (Bivalvia: Veneracea) in the Bahia de Yaldad, Isla de Chiloe, Southern Chile. J Exp Mar Biol Ecol 177:171-186

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461-488

de Klerk LG (1983) Sea levels, reefs and coastal plains of Southwest Sulawesi, Indonesia; a morphogenetic-pedological study. Ph.D. thesis, University of Utrecht, p 172

Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastarea annularis*. Ecol Monogr 77:3-18

Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Risk MH (1998) Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. Mar Pollut Bull 36:671-630

Erdmann N (1995) The ABC guide to coral reef fisheries in Southwest Indonesia, Sulawesi. Naga, the ICLARM Quaterly, 18:4-6

Fong P, Glynn PW (1998) A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? Mar Biol 130:663-674

Fox HE (2004) Coral recruitment in blasted and unblasted sites in Indonesia: assessing rehabilitation potential. Mar Ecol Prog Ser 269:131-139

Gardner TA, Cote I, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958-960

Gilmour JP (2002a) Substantial asexual recruitment of mushroom corals contributes little to population genetics of adults in conditions of chronic sedimentation. Mar Ecol Prog Ser 235:81-91

Gilmour JP (2002b) Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. Mar Freshw Res 53:805-812

Gilmour JP (2004) Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. Coral Reefs 23:494-504

Glassom D, Zahai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar Biol 144:641-651

Gleason MG (1996) Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. J Exp Mar Biol Ecol 207:79-101

Goffredo S, Chadwick-Furman NE (2003) Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea. Mar Biol 142:411-418

Goffredo S, Mattioli G, Zaccanti F (2004) Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Coral Reefs 23:433-443

Green EP, Shirley F (1999) The global trade in corals. World Conservation Monitoring Centre, World Conservation Press, Cambridge UK, p60

Grigg RW (1976) Fisheries management of precious and stony corals in Hawaii. Sea Grant Technical Report 77/03, University of Hawaii, p1-48

Grigg RW (2001) Black coral: history of a sustainable fishery in Hawaii. Pac Sci 55:291-299

Harriott VJ (1992) Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. Coral Reefs 11:215-219

Hoeksema BW (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zool Verh Leiden 254:1-295

Hoeksema BW (2004) Impact of budding on free-living corals at East Kalimantan, Indonesia. Coral Reefs 23:492

Hoeksema BW, Moka W (1989) Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. Net J Sea Res 23:149-160

Hughes TP (1984) Population dynamics based on individual size rather then age: a general model with a reef coral example. Am Nat 123:778-795

Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70:275-279

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141-166

Hughes TP, Connell JH (1987) Population dynamics based on size or age? A reef-coral analysis. Am Nat 129:818-829

Hughes TP, Bellwood DR, Connolly SR (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol Lett 5:773-784

Huston M (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19-25

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. UNESCO, Paris, pp 529-541

Knittweis L (2008) Population Demographics and Life History Characteristics of *Heliofungia actiniformis*, a Fungiid Coral Species Exploited for the Live Coral Aquarium Trade in the Spermonde Archipelago, Indonesia. Ph.D. thesis, University of Bremen

Knittweis L, Kraemer WE, Timm J, Kochzius M (2008) Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. Conserv Genet [doi: 10.1007/s10592-008-9566-5]

Krupp DA, Jokiel PL, Chartrand TS (1992) Asexual reproduction by the solitary scleractinian coral *Fungia scutaria* on dead parent coralla in Kanehoe Bay, Ohahu, Hawaiian Islands. Proc 7th Int Coral Reef Symp 1:527-534

Lamberts AE (1978) Coral growth: alizarin method. In: Stoddart DR, Johannes RE (eds) Coral reefs: research methods. UNESCO, Paris, p 523-527

Lewis JB (1989) Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. Coral Reefs 7:161-167

Lewis JB (1997) Abundance, distribution and partial mortality of the massive coral *Siderastrea siderea* on degrading coral reefs at Barbados, West Indies. Mar Pollut Bull 34:622-627

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400-417

Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar Ecol Prog Ser 209:43-54

Miller MW (1995) Growth of a temperate coral: effects of temperature, light, depth and heterotrophy. Mar Ecol Prog Ser 122:217-225

Moll H (1983) Zonation and diversity of Scleractinia on reefs off S.W. Sulawesi, Indonesia. Ph.D. thesis, University of Leiden, p 107

Munro JL (1982) Estimation of the parameters of the von Bertalanffy growth equation from recapture data at variable time intervals. ICES J Mar Sci 40:199-200

Munro JL, Pauly D (1983) A simple method for comparing the growth of fishes and invertebrates. ICLARM Fishbyte 1:5-6.

Nacua SS, Alino PM (1994) Comparison on the colonization and recruitment of algae and sessile (sic) on three different types of recruitment plates at two sites in Bolinao, Pangasinan, Philippines. Bull Mar Sci 55:1347-1348

Pet-Soede C, Van Desen WLT, Hiddink JG, Kuyl S, Machiels MAM (2001) Can fishermen allocate their fishing effort in space and time on the basis of their catch rates? An example from Spermonde Archipelago, S.W. Sulawesi, Indonesia. Fisheries Manag Ecol 8:15-36

Pauly D (1984) Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Stud Rev 8:325

Plaut I, Fishelson L (1991) Population structure and growth in captivity of the spiny lobster *Panulirus penicillatus* from Dahab, Gulf of Aqaba, Red Sea. Mar Biol 111:467-472

Raymakers C (2001) Review of the trade in live corals from Indonesia. Traffic International Cambridge

Reyes MZ, Yap HT (2001) Effect of artificial substratum material and resident adults on coral settlement patterns at Danjugan Island, Philippines. Bull Mar Sci 69:559-566

Ross MA (1984) A quantitative study of the stony fishery in Cebu, Philippines. Mar Ecol - PSZN 5:75-91

Sparre P, Venema SC (1998) Introduction to tropical fish stock assessment. FAO Fish Tech Pap 306/1

Tomascik T, Mah AJ, Nontji A, Moosa MK (1997) The ecology of the Indonesian Seas, Part One. The ecology of Indonesia series, Volume VII. Periplus, Singapore

Tsounis G, Rossi S, Gili JM, Arntz W (2006) Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). Mar Biol 149:1059-1070

Tsounis G, Rossi S, Gili JM, Arntz W (2007) Red coral fishery at the Costa Brava (NW Mediterranean): case study of an overharvested precious coral. Ecosystems 10:975-986

von Bertalanffy L (1938) A quantitative theory of organic growth (Inquiries on growth laws. II). Hum Biol 10:181-213

Vermij MJA, Bak RPM (2002) Inferring demographic processes from population size structure in corals. Proc 9th Int Coral Reef Symp 1:598-593

Wabnitz C, Taylor M, Green E, Razak T (2003) From ocean to aquarium. From ocean to aquarium. United Nations Environment Program/World Conservation Monitoring Centre. Cambridge

Wallace CC (1985) Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. Mar Ecol Prog Ser 21:289-298

Wilkinson CR (ed) (2004) Status of coral reefs of the world. Global Coral Reef Monitoring Network, Australian Institute of Marine Science, Townsville

Yamashiro H, Nishihira M (1998) Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. J Exp Mar Biol Ecol 225:253-267

Chapter 3

Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts

Juvenile ***Heliofungia actiniformis***

Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts

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Abstract

The fungiid *Heliofungia actiniformis* is one of the most popular scleractinian coral species in the growing live aquarium trade, with the majority of specimens originating in Indonesia. Details on population connectivity may potentially provide important information with regards to harvest management efforts. Genetic structure was examined, using ribosomal ITS1, 5.8S and partial ITS2 sequences on a small scale among populations in the Spermonde Archipelago, South Sulawesi (up to 65 km distance, Φ_{st}=0.09), and on a large scale throughout the Indo-Malay Archipelago (up to 2,900 km distance, Φ_{st}=0.26). Significant genetic structuring was found at both scales. Within the Spermonde Archipelago isolation by distance as well as local oceanographic features shaped patterns of genetic connectivity. On the large scale, the data revealed genetically distinct populations in Tomini Bay, New Guinea and the Thousand Islands near Jakarta, and a lack of genetic differentiation among populations lying close to or directly in the path of the Indonesian throughflow: from the central Visayas to the Flores Sea (Φ_{ct}=0.32). Whilst the influence of both historical and present day processes on genetic structuring of *H. actiniformis* populations was revealed, large scale results further emphasised the importance of oceanographic dynamics on larval dispersal patterns in this species. Potential for larval input from surrounding populations and the increased vulnerability of upstream as well as isolated populations should be taken into consideration when setting future harvest quotas.

Keywords: mushroom coral; larval source; genetic variation; larval dispersal; Indo-Pacific

Introduction

Marine ornamental species are collected around the world to supply specimens for the international aquarium trade, which is estimated to be worth 200-330 million US$ annually. Indonesia is the world's largest exporter of live marine ornamental corals since the 1980s (Wabnitz et al. 2003) and *Heliofungia actiniformis* ranks in the top five of all coral species being exploited for the live coral market (Green and Shirley 1999). An export quota system is in place, but knowledge on the population ecology of this species is limited (Abe 1937, 1940), and altogether lacking for the Indo-Malay Archipelago. Yet if harvesting regimes are to be sustainable in the long term, the exploited populations need to be self-sustaining, i.e. recruitment needs to exceed mortality and polyp collection. An indication of the extent of population connectivity provided by dispersing larvae is thus important with regards to the design of successful fishery management recommendations.

Due to the inherent difficulty in studying coral larval dispersal pathways *in situ*, most information to date has come from the study of the indirect effects of larval dispersal on the genetic differentiation and gene flow among populations (e.g. Ayre and Hughes 2000; Nishikawa et al. 2003; Magalon 2005; Vollmer and Palumbi 2007). However, a number of factors have been implicated in shaping present-day genetic structure of marine populations, including the roles of (1) larval dispersal capabilities (Ayre and Hughes 2000; Lourie et al. 2005), (2) present day physical oceanographic features (Williams and Benzie 1996; Rodriguez-Lanetty and Hoegh-Guldberg 2002), and (3) historical events (Nelson et al. 2000; Barber et al. 2002).

The dispersal potential of scleractinian coral species is influenced by the mode of sexual reproduction: in oviparous species this involves broadcast spawning of pelagic gametes, in viviparous species the release of brooded planulae. While brooded planulae generally settle within 1-2 days of release, planulae from spawning corals require 4-6 days after gamete release before they settle (see review by Harrison and Wallace 1990). The only existing study on the reproductive characteristics of *H. actiniformis* to date found that well developed, brooded larvae were released by the mother polyps. The larvae showed negative phototactic behaviour after 2 days and the great majority had attached to the substrates provided in the laboratory after 3 days (Abe 1937). In *H. actiniformis*, one may thus expect somewhat limited larval dispersal and potentially significant genetic structuring between neighbouring reef systems. However, it is known that coral larvae are able to prolong their competency periods if they do not encounter suitable substrate for settlement. Furthermore, although the larvae of brooding corals settle faster than those of broadcast spawners, their potential maximum competency periods are much longer due to the high energy reserves they can draw upon when needed (Richmond 1989; Wilson et al. 1998).

The oceanography of the Indo-Malay Archipelago is dominated by the Indonesian throughflow (ITF) current, which moves up to 19 million m^3 of water per second from the Pacific to the Indian Ocean (Gordan and Fine 1996; Gordon 2005). This current provides a potential dispersal corridor for marine larvae from the north-west Pacific along the Makassar Strait, all the way into the Flores and Banda Seas before finally being deflected to the Indian Ocean. Seasonally reversing east-west currents in the Java and Flores Seas moving at up to 75 cm s^{-1} (Wyrtki, 1961) should further facilitate present-day marine larval dispersal within the Indonesian Seas.

However, the complex geographical history of the Indo-Malay Archipelago (Tomascik et al. 1997) has in the past provided numerous opportunities for vicariance. Between 2.5 million and 10,000 years ago, sea levels fell repeatedly during multiple glaciations (Haq et al. 1987). During the height of the Pleistocene glacial period about 18,000 years ago, sea levels are thought to have dropped by 120 m (Voris 2000), greatly reducing the ITF and exposing both the Sunda and the Sahul continental shelf. Indeed, a number of studies have found the signatures of both the isolation of marine basins and postglacial re-colonisation events on the genetic structure of marine organisms in the Indo-Malay Archipelago (Nelson 2000; Barber et al. 2002; Sugama et al. 2002; Lourie et al. 2005).

Despite the central Indo-Pacific's ecological importance as the world's coral biodiversity hotspot (Hughes et al. 2002), and the subsistence value of local reef exploitation to millions of people, no previous investigations into patterns of genetic variation of scleractinian coral species in this region are known to the authors. Ribosomal internal transcribed spacer (ITS) sequences were used to (1) examine genetic variability and genetic affinities of *H. actiniformis* populations on a small scale, i.e. throughout the Spermonde Archipelago (South Sulawesi) among reefs 7-65 km apart and (2) examine genetic variability and genetic affinities of *H. actiniformis* populations on a large scale, i.e. throughout the Indo-Malay Archipelago among reefs up to 2,900 km apart. The implications of likely larval connectivity patterns are discussed in light of potential management approaches to the exploitation of this species for the coral aquarium trade.

Materials and methods

Collection of samples

Heliofungia actiniformis tentacle clippings were collected without further moving or harming the corals from a total of ten sites throughout the Indo-Malay Archipelago (Fig. 1). Nine locations were in Indonesia: Adi, Gilli Trawangan, Komodo, Manado, Pulau Seribu, Saboeda, Pulau Sembilan, Spermonde Archipelago, Tilamuta and one in the Philippines: Cebu. In the Spermonde Archipelago samples were collected from nearshore (Barrang Lompo, Samalona), midshelf (Lanyukang, Sarappokeke) and outershelf (Kapoposang) reefs. Wherever possible, tissue samples were collected from polyps at least 50 m apart and of different colour morphs to reduce the likelihood of sampling genetically identical clones. Tissues were stored in 96% ethanol at 4 °C. Variable numbers of samples collected reflect species abundance levels at sampling sites.

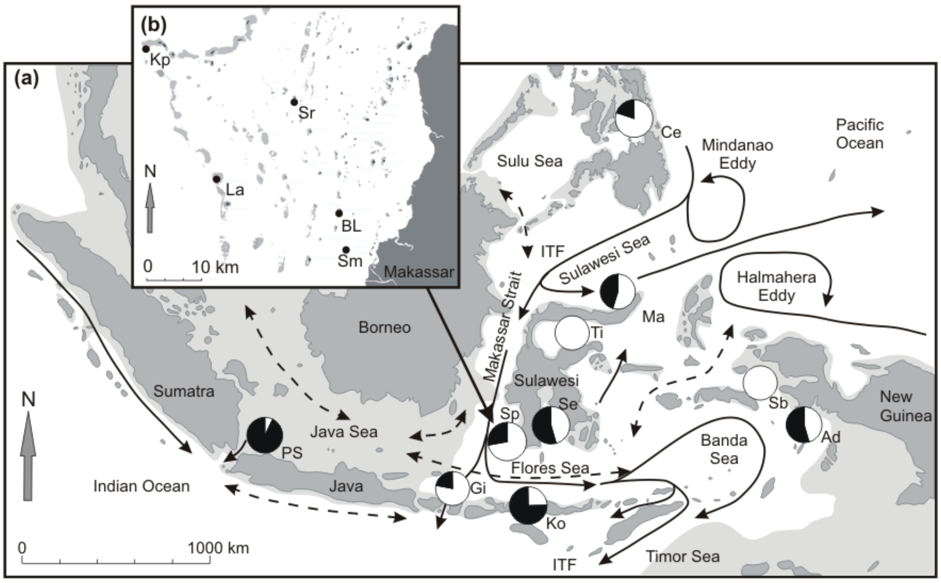

Fig. 1 (a) Sampling sites in the Indo-Malay Archipelago. Ad: Adi; Ce: Cebu; Gi: Gilli Trawangan; Ko: Komodo; Ma: Manado; PS: Pulau Seribu; Sb: Saboeda; Se: Pulau Sembilan; Sp: Spermonde; Ti: Tilamuta. Pie diagrams show frequencies of clades 1 and 2 (see Fig. 3; Spermonde data pooled). Arrows indicate dominant (solid) and seasonally changing (dashed) currents. Shaded areas represent shelf regions exposed during the Pleistocene (taken from Voris 2000). ITF: Indonesian Throughflow. **(b)** Sampling sites in the Spermonde Archipelago. BL: Barrang Lompo; Kp: Kapoposang; La: Lanyukang; Sm Samalona; Sr: Sarappokeke. Shaded areas represent present day reefs (taken from Landsat ETM+ satellite image, acquisition year 2002)

Extraction, PCR amplification, and sequencing of DNA

DNA was extracted with a 5% Chelex® solution (Walsh et al. 1991) and approximately 650 base pairs of the ITS1-5.8S-ITS2 rDNA region were amplified by the polymerase chain reaction (PCR) using the coral specific primer A18S (GATCGAACGGTTTAGTGAGG; Takabayashi et al. 1998a) and universal primer ITS-4 (TCCTCCGCTTATTGATATGC; White et al. 1990). The PCR reaction was carried out in a total volume of 50µl. PCR reactions contained 1 µl template DNA, 10 mM TrisHCl (pH 9), 50 mM KCl, 1.5 mM $MgCl_2$, 0.2 mM dNTP-mix, 0.4 mM of each primer, 40 µg BSA (bovine serum albumin) and 1 unit *Taq* polymerase (Promega). Amplification was performed in an Eppendorf Gradient S Thermal Cycler as follows: 30 cycles of 1 min at 94°C, 2 min at 55°C, 3 min at 72°C (Rodriguez-Lanetty and Hoegh-Guldberg 2002). Successfully amplified PCR fragments were purified using the peqGOLD Cycle Pure Kit (Safety-Line; PeqLab Biotechnology GmbH, Erlangen, Germany) following the instructions of the manufacturer. Sequencing of both strands was conducted with the PCR primers, the DyeDeoxy Terminator chemistry (PE Biosystems, Foster City, U.S.A.), and an ABI automated sequencer. No sequence ambiguities were found on both strands, indicating a lack of sequence heterogeneity between the multiple ITS copies and allowing direct sequence alignment and data analysis.

Data analysis

The obtained sequences were aligned with a sequence of *Siderastrea stellata* (Forsman et al. 2005) using ClustalW (Thompson et al. 1994) as implemented in the software BioEdit version 7.0.9 (Hall 1999) to delimit the ITS1, 5,.8S and ITS2 regions. The best fit model of nucleotide substitution was calculated by performing hierarchical likelihood ratio tests with Modeltest version 3.06 (Posada and Crandall 1998), and considered in subsequent analyses.

Inter- and intra-population genetic diversity indices, such as haplotype diversity (*h*) and nucleotide diversity (π) (Nei 1987), were calculated with the programme Arlequin version 3.11 (Excoffier et al. 2005). Population genetic structuring was further examined using the AMOVA algorithm as implemented in Arlequin. To examine the degree of gene flow between sampling sites, pairwise Φ_{st} were calculated by computing a distance matrix under consideration of the model that gave the best fit in Modeltest. A hierarchical AMOVA was subsequently carried out to look into potential population groupings according to geographic as well as oceanographic affinities.

Estimates of pairwise Φ_{st} were plotted against geographical distance and significance of the resulting correlation was determined by a Mantel test (Manly 1994) as well as reduced major axis regression, using Isolation by Distance (IBD) Web Service version 3.14 (Jensen et al. 2005; http://ibdws.sdsu.edu). Geographic distances consisted of the present-day shortest path by sea between any two populations, calculated in Google Earth version 4.0.13. Analyses had a nested design, with (1) small scale geographic variations investigated for sampling sites within the Spermonde Archipelago and (2) large scale geographic variations investigated for the Indo-Malay Archipelago.

A haplotype network based on pairwise sequence differences was created using the programme TCS version 1.21 (Clement et al. 2000). This method defines connections among haplotypes that have a cumulative probability of 95% of being true following the parsimony principle. Using these connections and the inferred missing intermediate stages, TCS plots a network and indicates the most likely root/ancestral haplotype. The network was further split into clades by dividing clusters of haplotypes separated by the largest number of mutational steps. Gaps in the alignment resulting from base insertion/deletion were treated as a fifth nucleotide state.

Results

Sequence Analysis

In total, 21 different haplotypes were defined by 22 polymorphic sites in 173 obtained sequences. The nucleotide sequences were submitted to the European Molecular Biological Laboratory (EMBL); accession numbers are AM849550-AM849570. The best fit model of nucleotide substitution was Jukes and Cantor + I (JC+I), with estimated base frequencies and invariable sites (i) of 0.9839. Within the 623 bp alignment, the length of ITS-1 was 239 bp (complete); 5.8S and ITS-2 were 157 bp (complete) and 217 bp (partial), respectively. The full ITS-1 segment was more variable than the partial ITS-2 segment, with an average variation of 7.9% and 1.4%, respectively, whilst the 5.8S region was identical in all sequences.

Genetic Diversity Measures

Haplotype diversity (*h*) within populations ranged from 0.40 at Saboeda to 0.87 at Lanyukang in the Spermonde Archipelago. Average nucleotide diversity (π) ranged from 0.0009 at Tilamuta to 0.0048 at Adi. Levels of haplotype and nucleotide diversity were not always correlated, the most striking example being Adi in New Guinea, which had one of the lowest haplotype diversities ($h = 0.5$), yet the highest nucleotide diversity (Table 1).

Table 1 Sampling localities, sample size and genetic diversity measures ± standard deviation (h = haplotype diversity; π = nucleotide diversity)

Sampling Site	**Acronym**	**n**	***h***	**π**
All	/	173	0.82 (±0.02)	0.0099 (±0.0052)
Adi	Ad	4	0.50 (±0.27)	0.0048 (±0.0038)
Barrang Lompo	BL	25	0.83 (±0.05)	0.0021 (±0.0015)
Cebu	Ce	31	0.68 (±0.08)	0.0025 (±0.0017)
Gilli Trawangan	Gi	9	0.69 (±0.15)	0.0025 (±0.0019)
Kapoposang	Kp	9	0.69 (±0.15)	0.0026 (±0.0019)
Komodo	Ko	8	0.82 (±0.10)	0.0036 (±0.0025)
Lanyukang	La	14	0.87 (±0.05)	0.0027 (±0.0019)
Manado	Ma	11	0.71 (±0.14)	0.0034 (±0.0023)
Pulau Seribu	PS	14	0.54 (± 0.11)	0.0015 (±0.0012)
Saboeda	Sb	5	0.40 (±0.24)	0.0020 (±0.0017)
Samalona	Sm	11	0.73 (±0.14)	0.0031 (±0.0022)
Sarapokeke	Sr	10	0.80 (±0.09)	0.0032 (±0.0022)
Pulau Sembilan	Se	11	0.78 (±0.12)	0.0032 (±0.0022)
Tilamuta	Ti	11	0.65 (±0.11)	0.0009 (±0.0009)

Population Subdivision

Weak but nonetheless significant genetic structuring was found within the Spermonde Archipelago ($\Phi_{st} = 0.093$, $p < 0.02$; Table 2). The pairwise Φ_{st} values revealed the largest genetic subdivision to be present between the site closest to the shore (Samalona) and the sites at the shelf-edge (Kapoposang, Lanyukang). A significant genetic structure was also found between the populations in Barrang Lompo and Kapoposang (Table 3).

Table 2 Analysis of Molecular Variance (AMOVA) results: Spermonde Archipelago. Φ_{st} = 0.093, p = 0.022

Source of Variation	Degrees of Freedom	Sum of squares	Variance component	% Variation
Among populations	4	7.680	0.08372	9.30
Within populations	64	52.262	0.81659	90.70
Total	68	59.943	0.90031	

Table 3 Matrix of pairwise population Φ_{st} values, Spermonde Archipelago. Sm: Samalona; BL: Barrang Lompo; Sr: Sarappokeke; La: Lanyukang; Kp: Kapoposang

	Sa	Bl	Sr	La	Kp
Sa	0.000				
Bl	0.070	0.000			
Sr	0.111	-0.006	0.000		
La	0.220**	0.075	0.062	0.000	
Kp	0.302**	0.190*	0.004	-0.042	0.000

* p<0.05, ** p<0.01

AMOVA showed high levels of genetic structuring in the Indo-Malay Archipelago (Φ_{st} = 0.26, p <0.0001; Table 4), indicating restricted gene flow between the populations investigated. Grouping the populations into the five groups (1) Adi (2) Barrang Lompo, Cebu, Gilli Trawangan, Manado, Kapoposang, Komodo, Lanyukang, Samalona, Sarappokeke, Pulau Sembilan (3) Pulau Seribu (4) Saboeda (5) Tilamuta, explained the maximum of the variation among the populations (Φ_{ct} = 0.32, p = 0.007; Table 5).

Table 4 Analysis of Molecular Variance (AMOVA) results: Indo-Malay Archipelago. Φ_{st} = 0.26, p = <0.0001

Source of Variation	Degrees of Freedom	Sum of squares	Variance component	% Variation
Among populations	13	53.895	0.27809	25.92
Within populations	159	126.379	0.79484	74.08
Total	172	180.274	1.07293	

Table 5 Hierarchical Analysis of Molecular Variance (AMOVA) groupings. Ad: Adi; BL: Barrang Lompo; Ce: Cebu; Gi: Gilli Trawangan; Ko: Komodo; Kp: Kapoposang; La: Lanyukang; Ma: Manado; PS: Pulau Seribu; Sb: Saboeda; Se: Pulau Sembilan; Sm: Samalona; Sr: Sarappokeke; Ti: Tilamuta

Grouped Populations	**Φ_{ct}**
(BL, Ce, Gi, Ko, Kp, Ma, Se, Sm, Sr) (Ad) (PS) (Sb) (Ti)	0.32^{**}
(BL, Ce, Gi, Ko, Kp, Ma, Sm, Sr) (Ad) (PS) (Se) (Sb) (Ti)	0.28^{**}
(BL, Ce, Gi, Ko, Kp, Ma, Se, Sm, Sr) (Ad, Sb) (PS) (Ti)	0.23^{*}
(BL, Ce, Gi, Ko, Kp, Ma, Sm, Sr) (Ad, Sb) (PS) (Se) (Ti)	0.20^{*}
(BL, Ce, Gi, Ko, Kp, Ma, Sm, Sr) (Ad, Sb, Se) (PS) (Ti)	0.17^{*}
(BL, Ce, Gi, Ko, Kp, Ma, Se, Sm, Sr) (Ad, Sb, Ti) (PS)	0.15^{*}
(BL, Gi, Ko, Kp, Ma, Se, Sm, Sr) (Ad, Sb) (Ce) (PS) (Ti)	0.14
(BL, Gi, Ko, Kp, Se, Sm, Sr) (Ad, Sb) (Ce, Ma) (PS) (Ti)	0.14
(BL, Ce, Gi, Ko, Kp, Ma, Sm, Sr) (Ad, Sb, Ti) (Se) (PS)	0.12
(BL, Ce, Gi, Ko, Kp, Ma, Sm, Sr) (Ad, Sb, Se, Ti) (PS)	0.12
(BL, Gi, Ko, Kp, PS, Se, Sm, Sr,) (Ad, Sb) (Ce, Ma) (Ti)	0.06

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

Isolation by distance analyses (Fig. 2) revealed a significant increase in genetic diversity with increasing geographic distance on the small scale within the Spermonde Archipelago as well as across the Indo-Malay Archipelago.

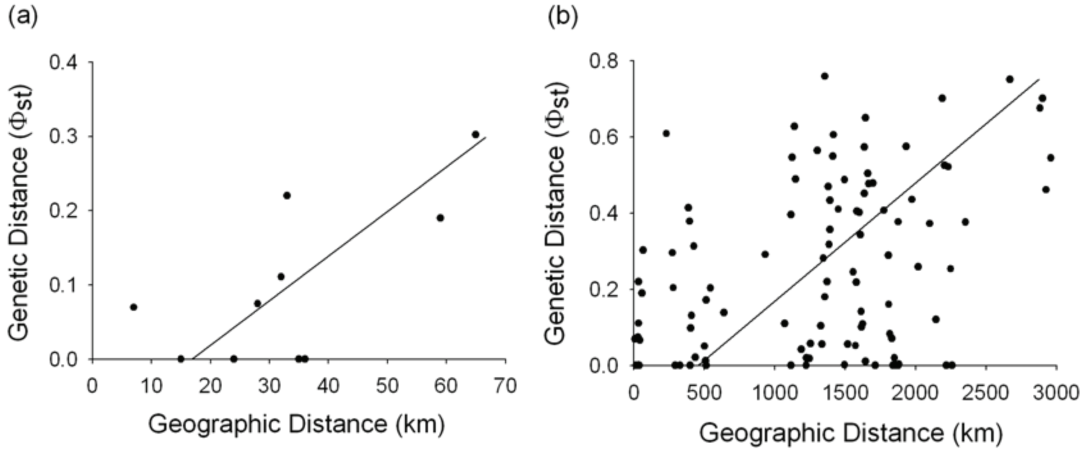

Fig. 2 Isolation-by-distance plots **(a)** Spermonde Archipelago; $y=-0.1071+6.106^{-03}x$, $r=0.69$, $R^2=0.48$, $p=0.0427$. **(b)** Indo-Malay Archipelago; $y=-0.1021+3.016^{-04}x$, $r=0.45$, $R^2=0.2$, $p=0.0104$. Negative genetic distances were set to zero

Of the 21 haplotypes, 10 were singletons and of the remaining 11 haplotypes, 8 were shared among populations. One haplotype occurred in 34% of all samples and was found in 13 populations. The minimum-spanning network revealed two clades, separated by six mutational steps (Fig. 3). Clade one contained haplotypes from Adi, Cebu, Gilli Trawangan, Komodo, Manado, Pulau Seribu, Pulau Sembilan, and Spermonde. Haplotypes from clade two (63% of total) were present in all populations (Fig. 1).

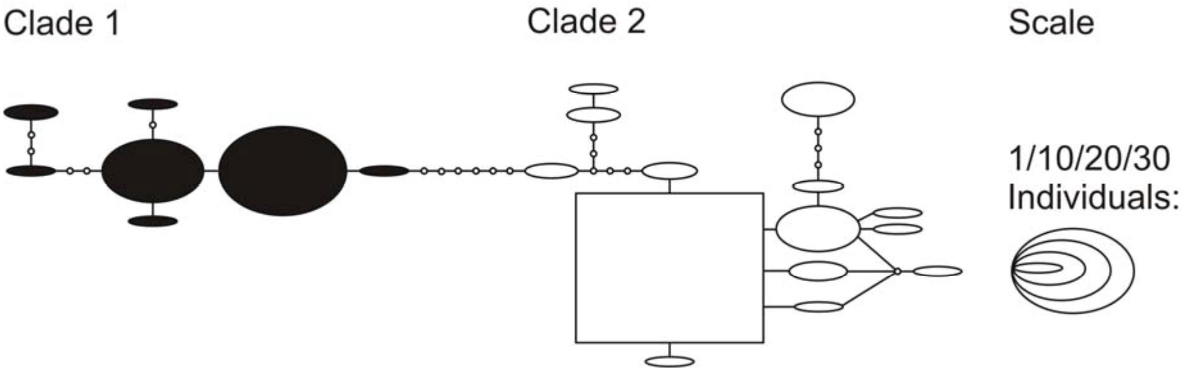

Fig. 3 Unrooted minimum-spanning network showing 21 haplotypes grouped into two clades. Square: ancestral haplotype (n=59). Size of ovals/square: proportional to haplotype frequencies. Lines represent single mutational steps, empty circles missing intermediate haplotypes

Discussion

Small scale genetic differentiation: Spermonde Archipelago

The significant genetic structure within the Spermonde Archipelago points to limited larval exchange on a small scale: the average distance over which limited dispersal was noted in this study is 52 km. Similarly restricted gene flow in brooding coral species has been found in other studies. For instance *Seriatopora hystrix* exhibits high levels of genetic differentiation along a 90 km stretch of the Great Barrier Reef (Ayre and Dufty 1994) and *Pocillopora damicornis* shows significant genetic subdivision among seven sites surrounding Lord Howe Island on the East Coast of Australia separated by only 1-6.5 km (Miller and Ayre 2004). Previous studies on the genetic structure of marine population genetics within Spermonde Archipelago found no restricted gene flow for the giant clam *Tridacna crocea* (Nuryanto and Kochzius 2006) and the stomatopod *Haptosquilla pulchella* (Barber et al. 2002) using mitochondrial COI sequences. However, both species have significantly longer planktonic larval phases: up to 14 days for *T. crocea* (Lucas 1994) and 4-6 weeks for *H. pulchella* (Barber et al. 2002).

The significantly different pairwise Φ_{st} values for the sites with the largest geographic separation and the fact that the data follow the isolation by distance model indicate that geographic separation is an important factor for the degree of larval connectivity between the populations sampled in Spermonde (Fig. 2a). However, a closer look at the data also points towards an influence of local current patterns on local larval exchange patterns. Although detailed information on the oceanography of the Spermonde Archipelago is lacking, it is clearly influenced by the ITF, which passes through the Strait of Makassar. Sites located at or near to the shelf edge are likely to be subjected to stronger currents than those in shallower water located near the coastline (for a detailed bathymetric map of the Spermonde Archipelago see de Klerk, 1983). This may explain the lack of genetic structure found between the outershelf and midshelf populations of Kapoposang, Lanyukang, and Sarappokeke, which have a maximal geographic separation of 36 km. In contrast, gene flow between Samalona (nearshore) and Lanyukang (midshelf), separated by 33 km, is limited. Furthermore, whereas a number of private haplotypes were found in the nearshore populations, none were present at the midshelf and outershelf sites. Such private haplotypes are most likely to develop in populations which have a limited exchange of larvae with surrounding populations (Barber et al. 2006), again supporting the notion of more isolated nearshore populations of *H. actiniformis* in the Spermonde Archipelago.

Large scale genetic differentiation: Indo-Malay Archipelago

At the large scale of the Indo-Malay Archipelago, long-distance gene flow between the Central Visayas and populations as far away as those in the Flores Sea was contrasted by regionally isolated populations in New Guinea, Tomini Bay, and the Java Sea. The presence of one large population with only limited genetic structure spanning the central part of the Indonesian Seas further supports the importance of current patterns in *H. actiniformis* larval dispersal: all populations lie very close to or directly in the path of the ITF current. A similar lack of genetic differentiation over a distance of 700 km was found for the coral *Pleisiastrea versipora* within the Ryuku Archipelago by Rodriguez-Lanetty and Hoegh-Guldberg (2002), who suggested dispersal aided by the strong Kuroshio Current as a likely explanation. Furthermore, within the Indo-Malay Archipelago, high levels of gene flow have previously been found along the path of the ITF: from North-Eastern Borneo to Southern Sulawesi for the prawn *Panaeus monodon* (Sugama et al. 2002), from Northern Sulawesi and Northern Borneo to South Sulawesi for the boring giant clam *Tridacna crocea* (Nuryanto and Kochzius 2006), from Northern Sulawesi to the Flores Sea for the stomatopods *Haptosquilla glyptocerus* and *Gonodactylinus viridis* (Barber et al. 2006), and from Cebu in the Philippines to West Timor for the pink anemonefish *Amphiprion perideraion* (Hamid 2007).

Considering the ITF reaches current strengths of up to 1 m s^{-1} (Wyrtki 1961) and the potentially long competency periods of brooded coral larvae (Richmond 1989), it is conceivable that *H. actiniformis* larvae are carried all the way from the Philippines to the distant reefs in the Flores Sea. However, it is more likely that dispersal is occurring via a series of stepping stones (Kimura and Weiss 1964). This notion is given support by the significant isolation by distance analysis at the large scale of the Indo-Malay Archipelago and the genetic break between the Flores Sea and New Guinea. Although the populations at Adi and Saboeda are potentially connected to those in the Flores Sea by an offshoot of the ITF (Fig. 1), potential stepping stones are lacking over considerable distances in this region. The limited number of samples collected in New Guinea combined with the curious presence of genetic differentiation between Adi and Saboeda, despite the islands' proximity and the presence of linking currents between the two sites (Gordon 2005), does however suggest that the results should be treated with some caution.

H. actiniformis populations in Tomini Bay were genetically dissimilar to all other populations sampled in this study. This is a region with numerous endemic species (Wallace et al. 2003), and a similar pattern of restricted gene flow with surrounding populations was found in *H. pulchella* by Barber et al. (2002). A likely explanation lies in the oceanographic properties of the area: there are no major currents driving an exchange of water masses with the neighbouring Malukku Sea (Gordon 2005). However, a genetic break between the neighbouring Java and Flores Sea *H. actiniformis* populations was also found, despite the presence of seasonally reversing currents in this region (Fig. 1). Indeed, a number of studies found similar genetic structuring between populations lying on the Sunda Shelf's Java Sea and those in the Flores Sea (Lourie et al. 2005; Barber et al. 2006; Nuryanto & Kochzius 2006; Timm & Kochzius 2006; Hamid 2007). The most likely explanation is that these populations may still carry the genetic signature of re-colonisation events on the Sunda Shelf at the end of the last glacial period. As *H. actiniformis* is absent from the South China Sea but present on the western shores of Sumatra and Java (Veron 2000), re-colonisation may have come from populations in the Indian Ocean. This would agree with results from Timm and Kochzius (2006), who found high levels of gene flow between *Amphiprion ocellaris* populations on the Sunda Shelf and in the Indian Ocean. However, an extension of the current sampling regime into the Indian Ocean and at more sites on the Sunda Shelf would be needed to confirm this hypothesis.

Barber et al. (2000) found sharp genetic breaks among populations of the mantis shrimp *Haptosquilla pulchella* in oceanographic regions in Indonesia, including populations north/south of the Java and Flores Seas only 300 km apart. This distribution of genetically distinct populations strongly reflects the historical isolation of sea-basins during the Pleistocene, which led the authors to suggest the presence of a marine Wallace line running perpendicular to the terrestrial Wallace line, which separates eastern and western Indonesia. Whilst the results of the present study also reflect patterns of historical events, the influence of oceanographic dynamics seems to be more acute in *H. actiniformis*, and since there were no sharp genetic breaks between populations at Spermonde/Sinjai and the Gilli Islands/Komodo, the notion of a marine Wallace line is not supported by the present results.

The revealed pattern of two major clades (Fig. 3) supports the hypothesis that re-colonisation after the Pleistocene came from the Indian Ocean: on the Sunda Shelf 93% of the haplotypes sampled belonged to clade 2. Also striking are the populations in Tomini Bay and at Saboeda (New Guinea), both of which only contained clade 1 haplotypes. Molecular genetic analyses of starfish (Williams and Benzie 1998; Benzie 1999; Kochzius et al. 2006), crustaceans (Duda and Palumbi 1999; Barber et al. 2002; Benzie et al. 2002) and fish (Bernardi et al. 2001, Timm and Kochzius 2006) all found a clear break between Indian and Pacific Ocean populations. In *H. actiniformis*, clade 1 haplotypes may have originated in the Pacific Ocean and the clade 2 haplotypes in the Indian Ocean. Subsequent dispersal and mixing processes could have generated the modern day distribution patterns of the two clades. This would also agree with existing taxonomic appraisals of scleractinian corals in the region, which have indicated biogeographic patterns consistent with speciation events in the Indian and Pacific Oceans and ensuing dispersal into the central Indo-West Pacific (Wallace 1997).

Furthermore, in terms of haplotype diversity, more diverse populations were found in these areas of presumed mixing, with Lanyukang (Spermonde) > Barrang Lompo (Spermonde) > Komodo, than on the periphery, where Saboeda < Adi < Pulau Seribu (Table 1). Patterns of nucleotide diversity somewhat mirrored these findings, with high values for Komodo > Manado > Sarapokeke (Samalona)/Pulau Sembilan, where a frequent input of larvae from neighbouring populations is more likely than at the sites with lower values: Tilamuta < Pulau Seribu < Saboeda (Table 2). Benzie et al. (2002) likewise found diversity measures to be five times that of the average in the geographic centre of *Penaeus mondon* distribution and suggested the evolution of genetic variants in peripheral populations and their subsequent migration into the Indo-Malay Archipelago to be responsible for this pattern. Together with the present study the patterns seem to lend support to the notions of a centre of overlap/a centre of accumulation to explain the presence of a regional centre of maximum marine biodiversity (see Hoeksema 2007 for a review).

Conspicuous in the present study is the population at Adi off western New Guinea. Here one of the lowest haplotype diversities (0.5) was contrasted by the highest nucleotide diversity (0.014) measured for all *H. actiniformis* populations investigated. It is feasible that haplotype variation is so limited due to the extreme rarity of mixing events at this location, but that the occasional input of larvae comes from three very different sources: the nearby Malukku Sea, the Banda Sea (via the ITF) and the Torres Strait. However, more detailed information on local oceanographic patterns and more samples from New Guinea are needed to draw firm conclusions.

Conclusions and management implications

The emerging pattern of *H. actiniformis* genetic population structure is thus highly complex, with the underlying pattern of isolation by distance confounded by historical and contemporary oceanographic factors as expected, especially at the scale of the Indo-Malay Archipelago (Fig. 2b). The results do however for the first time give an indication of the present-day levels of population connectivity for *H. actiniformis* and presumably scleractinian coral species with similar ecological features in the Indo-Malay Archipelago, and can thus help to inform conservation and trade management decisions.

The apparent larval seeding of downstream ITF populations has several management implications. Firstly, harvesting at upstream populations should be limited and done with caution: over-harvested populations are likely to have slower recovery rates due to the more limited input of larvae into the system. Secondly, no-take areas at these locations are particularly important as they may serve as larval source regions. Although further research considering scleractinian coral species with a variety of reproductive modes is needed, the results of this study suggest existing reserves such as the chain of marine protected areas along the eastern and southern coast of Negros (Philippines), the Turtle Islands Park in northeast Borneo (Malaysia) and the National Park in Bunaken (Indonesia) (Spalding et al. 2002) should be strengthened, enlarged and ideally multiplied to support conservation efforts in the coral triangle.

Whilst it might be tempting to set less stringent quotas for those populations apparently lying downstream of potential source populations, restricted gene flow may occur within local reef systems, as evidenced by the pattern found within the Spermonde Archipelago in the present study, and also for coral populations within the Great Barrier Reef (Ayre et al. 1997, 2000). In the case of the Spermonde Archipelago, more stringent quotas should be set for nearshore reefs, where a larval input via the ITF is less likely than for mid- and outershelf reefs. More generally, the results underline the importance of considering the detailed characteristics of each harvesting area separately to achieve long term sustainability.

Finally, as for the upstream populations, isolated populations not connected by suitable stepping stones and/or sufficiently strong current regimes, should be treated with extreme prudence when harvesting quotas are set. The government of Gorontalo province is currently considering whether to encourage fishermen to engage in the ornamental trade (personal communications, Leyla Knittweis). Since the population in Tomini Bay is genetically isolated, collection of *H. actiniformis* and presumably a number of other scleractinian coral species should be restricted and carefully monitored.

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References

Abe N (1937) Post-larval development of *Fungia actiniformis*. Palao Trop Biol Stn Stud 1:73-9

Abe N (1940) Growth of *Fungia actiniformis* var. palawensis Doederlein and its environmental conditions. Palao Trop Biol Stn Stud 2:105–145

Ayre DJ, Dufty S (1994) Evidence for restricted gene flow in the viviparous coral *Seriatopora hystrix* on Australia’s Great Barrier Reef. Evolution 48(4): 1183-1201

Ayre DJ, Hughes TP, Standish RJ (1997) Genetic differentiation, reproductive mode, and gene flow in the brooding coral *Pocillipora damicornis* along the Great Barrier Reef, Australia. Mar Ecol Prog Ser 159:175-187

Ayre DJ, Hughes TP (2000) Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54: 1590-1605

Barber PH, Palumbi SR, Erdmann MV, Moosa KM (2000) Biogeography: a marine Wallace’s line? Nature 406: 692-693

Barber PH, Palumbi SR, Erdmann MV, Kasim Moosa M (2002) Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. Mol Ecol 11:659-674

Barber PH, Erdmann MV, Palumbi SR (2006) Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the coral triangle. Evolution 60(9):1825-1839

Benzie JAH (1999) Genetic structure of coral reef organisms: ghosts of dispersal past. Am Zool 39:131-145

Benzie JAH, Ballment E, Forbes AT, Demetriades NT, Sugama K, Haryanti, Moria S (2002) Mitochondrial DNA variation in the Indo-Pacific populations of the giant tiger prawn *Panaeus monodon*. Mol Ecol 11:2553-2569

Bernardi G, Holbrook SJ, Schmitt RJ (2001) Gene flow at three spatial scales in a coral reef fish, the three spot dascyllus, *Dascyllus trimaculatus*. Mar Biol 138: 457-465

Clement M, Posada D, Crandall KA (2000) TCS: a programme to estimate gene genealogies. Mol Ecol 9:1657-1660

De Klerk LG (1983) Sea levels, reefs and coastal plains of Southwest Sulawesi, Indonesia; a morphogenetic-pedological study. Dissertation, State University of Utrecht

Duda TF Jr, Palumbi SR (1999) Population structure of the black tiger prawn *Panaeus monodon*, among western Indian Ocean and western Pacific populations. Mar Biol 134:705-710

Excoffier L, Laval G, Schneider S (2005) Arlequin version 3.0: an integrated software package for population genetics data analysis. Bioinformatics Online 1:47-50

Forsman ZH, Guzman HM, Chen CA, Fox GE, Wellington GM (2005) An ITS region of *Sidastrea* (Cnidaria: Anthozoa): is *S. glynni* endangered or introduced? Coral Reefs 24(2):342-347

Gordon AL, Fine RA (1996) Pathways of water between the Pacific and Indian Oceans in the Indonesian seas. Nature 379:146-149

Gordon AL (2005) Oceanography of the Indonesian Seas and their throughflow. Oceanogr 18(4):15-27

Green EP, Shirley F (1999) The global trade in corals. World Conservation Monitoring Centre, World Conservation Press, Cambridge, UK

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95-98

Hamid LMO (2007) Genetic population structure of the pink anemonefish *Amphiprion perideraion* (Pomacentridae) in the Indo-Malay Archipelago. MSc Dissertation, University of Bremen

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Ecosystems of the World, vol. 25. Coral reefs Elsevier Science Publishers, Amsterdam, pp133-207

Haq BU, Hardenbol J, Vail PR (1987) Chronology of fluctuating sea levels since the Triassic. Science 235:1156-1167

Hoeksema BW (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema W (ed) Biogeography, time and place: distributions, barriers and islands, Topics in Geobiology 29:117-178.

Hughes TP, Bellwood DR, Connnolly SR (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol Lett 5:773-784

Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. BioMed Cent Genet 6:13

Kimura M, Weiss GH (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561-576

Kochzius M, Hauschild J, Kirchhoff S, Meyer-Wachsmuth I, Seidel C (2006) Congruence of genetic population structure in the blue starfish *Linckia laevigata* and its parasite *Thyca crystallina* in the central Indo-Malay Archipelago? In: Abstracts of the 6th European meeting of the International Society for Reef Studies (ISRS), Bremen, Germany,19-22

Lourie SA, Green DM, Vincent ACJ (2005) Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: Hippocampus). Mol Ecol 14:1073-1094

Lucas JS (1994) The biology, exploitation and mariculture of giant clams (Tridacnidae). Rev Fish Sci 2:181-223

Magalon H, Adjeroud M, Veuille M (2005) Patterns of genetic variation do not correlate with geographical distance in the reef-building coral *Pocillopora meandrina* in the South Pacific. Mol Ecol 14:1861-1868

Manly BJF (1994) Multivariate statistical methods: a primer. Chapman and Hall, New York

Miller KJ, Ayre DJ (2004) The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. Heredity 92:557-568

Nelson JS, Hoddell RJ, Chou LM, Chan WK, Phang VPE (2000) Phylogeographic structure of the false clownfish, *Amphiprion ocellaris*, explained by sea level changes on the Sunda Shelf. Mar Biol 137:727-736

Nei M (1987) Molecular evolutionary genetics. Columbia University Press, New York

Nishikawa A, Katoh M, Kazuhiko S (2003) Larval settlement and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. Mar Ecol Prog Ser 256:87-97

Nuryanto A, Kochzius M (2006) Limited gene flow in the giant clam *Tridacna crocea* across the Indo-Malay Archipelago. In: Abstracts of the 6th European meeting of the International Society for Reef Studies (ISRS), Bremen, Germany, 19-22 September 2006

Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14:817-818

Richmond RH (1989) Competency and dispersal of spawned versus brooded coral planula larvae. Paper presented at the 6th International Coral Reef Symposium, Townsville, Australia, 08-12 September 1988

Rodriguez-Lanetty M, Hoegh-Guldberg O (2002) The phylogeography and connectivity of the latitudinally widespread scleractinian coral *Pleisiastrea versipora* in the Western Pacific. Mol Ecol 11:1177-1189

Spalding MD, Ravilious C, Green EP (2001) World atlas of coral reefs. UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA

Sugama K, Haryanti, Benzie JAH, Ballment E (2002) Genetic variation and population structure of the giant tiger prawn, *Penaeus monodon*, in Indonesia. Aquaculture 205:37-48

Takabayashi M, Carter D, Ward S, Hoegh-Guldberg O (1998) Inter- and intra-specific variability in ribosomal DNA sequence in the internal transcribed spacer region of corals. In: Greenwood JG, Hall NJ (eds) Proceedings of the Australian Coral Reef Society 75th Anniversary Conference, The University of Queensland, Brisbane, 1997

Thompson JG, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Res 22:4673–4680

Timm J, Kochzius M (2006) Strong genetic structure and limited gene flow between populations of the False Clown Anemonefish (*Amphiprion ocellaris*) in the Indo-Malay Archipelago. In: Abstracts of the 6th European meeting of the International Society for Reef Studies (ISRS), Bremen, Germany, 19-22 September 2006

Tomascik T, Mah AJ, Nontji A, Moosa MK (1997) The Ecology of the Indonesian Seas Part One. The Ecology of Indonesia Series Volume VII. Periplus, Singapore

Veron JEN (2000) Corals of the world. AIMS Townsville, Australia

Vollmer SV, Palumbi SR (2007) Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: Implications for the recovery of endangered reefs. J Hered 98(1):40-50

Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems, time durations. J Biogeogr 27:1153-1167

Wabnitz C, Taylor M, Green E and Razak T (2003) From ocean to aquarium. UNEP-WCMC, Cambridge, UK

Wallace CC (1997b) The Indo-Pacific centre of coral diversity re-examined at species level. Proceedings of the 8th International Coral Reef Symposium, Panama, 24-29 June, 1997

Wallace CC, Paulay G, Hoeksema BW, Bellwood DR, Hutchings PA, Barber PH, Erdmann M, Wolstenholme J (2003) Nature and origins of unique high diversity reef faunas in the Bay of Tomini, Central Sulawesi: The ultimate 'centre of diversity'? Proceedings of the 9th International Coral Reef Symposium, Bali, 23-29 October 2000

White TJ, Bruns T, Lee S, Taylor WJ (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications, Academic Press, San Diego, pp315-322

Walsh PS, Metzger DA, Higuchi R (1991) Chelex-100 as a medium for simple extraction of DNA for PCR based typing from forensic material. Biotechniques 10:506-513

Williams ST, Benzie JAH (1996) Genetic uniformity of widely separated populations on the coral reef starfish *Tinckia laevigata* from the East Indian and West Pacific Oceans, revealed by allozyme electrophoresis. Mar Biol 126:99-107

Williams ST, Benzie JAH (1998) Evidence of a biogeographic break between populations of a high dispersal starfish: congruent regions within the Indo-West Pacific defined by colour morphs, mtDNA, and allozyme data. Evolution 52(1):87-99

Wilson JR, Harrison PL (1998) Settlement-competency periods of larvae of three species of scleractinian corals. Mar Biol 131:339-345

Wyrtki K (1961) Physical oceanography of the Southeast Asian waters. Naga Report 2, Scripps Institution of Oceanography, p 195

Chapter 4

Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: potential future management approaches

Coral fisherman bringing in catch, Karangrang Island, Spermonde

Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: potential future management approaches

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Abstract

In 2004-2006 the Indonesian authorities allocated the highest live coral trade quotas in South Sulawesi to *Heliofungia actiniformis* despite a lack of data on biological characteristics and impacts of collection practices. Semi-structured interviews with fishermen and *in situ* surveys revealed a size-selective fishery towards small polyps, resulting in a shift in size-frequency distributions and reduced overall abundances at harvested sites. Total mortality rates were significantly higher compared to those known from unharvested sites for polyps sized 0-11 cm, with exploitation rates of 0.1 and 0.7 for polyps sized 0-4 cm, and 4-11 cm respectively. The application of a utility per recruit approach revealed maximum potential economic yield to occur at a size of 5 cm, corresponding to an age of 5 years. This is five years before the attainment of reproductive maturity and fifteen years before the attainment of maximum biomass yield per recruit. The Thompson and Bell predictive model indicated that in combination with a 5 cm size limit to curb current economic overfishing, reducing exploitation rates for polyps in the 4-11 cm size bracket to 0.5 through a reduction of harvest quotas would in fact be possible without lowering current profits. Achieving long term sustainability will in addition necessitate an effective protection of spawning stocks.

Keywords: Fungiidae, aquarium trade, marine ornamentals, fishery management, utility per recruit

Introduction

Marine ornamentals are collected around the world to supply specimens for the international aquarium trade, which is worth an estimated 200-330 US$ million annually (Wabnitz et al., 2003). Indonesia is the world's largest exporter of marine ornamental species since the 1980s, and in 2005 supplied an estimated 91% of the live coral on the world market (Wabnitz et al., 2003; Jones, 2008). Colourful, frequently large polyped coral species belonging to genera such as *Catalaphyllia*, *Euphyllia*, *Heliofungia*, *Plerogyra* and *Trachyphyllia* dominated the live coral trade from 1988 to 2002 (Wabnitz et al., 2003).

Indonesia is signatory to the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), and coral harvesting is managed through an annual harvest quota established separately for each region and species. Furthermore, the country's guidelines for the sustainable utilization of coral resources also stipulates best collection practices including size limits, rotation of collection sites and the prohibition of coral collection in marine parks and tourist areas (Bruckner, 2002). Unfortunately, although considerable effort has been directed towards assessing the amount and dynamics of international trade in marine ornamentals (Green and Shirley, 1999; Raymakers, 2001; Bruckner, 2002; Wabnitz et al., 2003; Jones, 2008), little effort has been devoted to the biological study of coral population demographics with the direct aim of designing appropriate management plans. Considering the scattered information available on the population dynamics of large-polyped scleractinian corals in particular, present day trade management efforts are lacking a scientific basis (Raymakers, 2001), effectively making current collection quotas arbitrary values.

This lack of data is at least partly due to the colonial nature of most scleractinian coral species, which may result in a distorted relationship of colony size and age due to processes such as colony fusion and fission (Hughes and Jackson, 1980; Chadwick-Furman et al., 2000), complicating the study of population dynamics. Relating size and age is however possible in a number of scleractinian corals with commercial value, for instance in species with compact or massive growth forms, or indeed aclonal polyps (e.g. *Heliofungia* and *Trachyphyllia*). In such corals age may either be a linear function of individual length, or, in species which grow determinately, age-size relationships need to be estimated by growth curves, such as the widely applied von Bertalanffy growth curve (von Bertalanffy, 1928; Chadwick-Furman et al., 2000; Goffredo and Chadwick-Furman, 2003; Knittweis et al. 2008). In these corals size/age frequency distributions reflect the combined effects of growth, survival and recruitment, and are thus a record of the population's life-history (Tsounis et al., 2006). Coral size structures may however also vary among populations of a particular species in different reef habitats (Vermeji and Bak, 2002) or as a result of disturbances including predator outbreaks (Done, 1987), storms and cyclones (Hughes, 1989; Gilmour, 2004), sedimentation regimes (Gilmour, 2004; Brown and Clarke, 2002), and water quality differences (Bak and Meesters, 1999; Meesters et al., 2001). Moreover, environmental factors may impact the frequency distributions of separate life history stages differently as it has been showed for mushroom corals (Gilmour, 2004), where a sessile growth phase with attached polyps is followed by a detached, free-living phase.

Where geographically adjacent sites, which minimize spatial variation in terms of environmental conditions and disturbances are available, harvested and unharvested sites may be compared using a control-effect design (Osenberg and Schmitt, 1996). A comparative analysis of harvested and unharvested sites will then allow inferences on the effects of a fishery on parameters such as (1) overall abundances (2) shifts in size/age distributions (3) reproductive potential of remaining individuals (where complementary data on reproductive biology is available) and (4) natural/fishing mortalities and related exploitation rates to be made. Based on such data the potential for long term sustainability of harvesting activities can be evaluated, and management suggestions made (Grigg, 1976; Ross, 1984; Grigg, 2001; Tsounis et al., 2006).

In addition, fisheries yield models can be applied to search for the best harvesting strategy. The Beverton and Holt model (1957) or its predecessor, the Thompson & Bell table calculation approach (1934) allow for the calculation of maximum potential yield per recruit (Y/R). The Beverton and Holt model in particular has been advocated as a viable management approach to the exploitation of coral populations (Chadwick-Furman et al., 2000; Goffredo et al., 2004). It computes the age of maximum biomass production of a cohort, corresponding to the optimal age/size for stock harvesting. Calculations are based on the species' demographic characteristics such as growth rates, the rates of natural and fishing mortality and the relationship between individual mass and length/age at first capture. Stock-recruitment effects are however not considered, instead there is the underlying assumption that recruitment rates will be maintained at the estimated sustainable harvest levels. While this approach has not yet not been applied to the management of a coral species exploited for the aquarium trade, potential maximum stock yields have been calculated for a number of anthozoan species (Grigg, 1984; Ross, 1984; Chadwick-Furman et al., 2000; Goffredo and Chadwick-Furman, 2003; Goffredo et al. 2004; Tsounis et al. 2007) and the black coral fishery of Hawaii provides a practical example of the successful application of this approach to the harvest of a precious coral stock (Grigg, 2001).

While a potential maximum yield and a corresponding optimal catch size may be derived from this approach, a viable management strategy may also require complimentary insight into socio-economic factors such as the location of preferred harvesting grounds, fishing methods, coral selection criteria during harvesting and subsequent sale, coral prices, adherence to current management schemes and so forth (Tsounis et al., 2007). Indeed, an application of the utility per recruit paradigm (Die et al., 1988), where the yield obtained at each age is weighted by a measure of its actual value may be more suited to the live coral trade, since maximising the total weight of the catch may in fact be less desirable than for instance harvesting corals of certain sizes or with bright colours.

The approach of Thompson and Bell (1934) has widely been used in finfish and invertebrate fisheries management to explore different harvesting strategies and thus find the combination of fisheries mortality and size/age at first capture that optimizes biological and/or economic yield from the fishery, since it allows for predictive calculations (e.g. Groeneveld, 2000; Kirchner, 2001; Nevarez-Martinez et al., 2006). Again, this has never been attempted with respect to live coral harvesting.

The aims of the present study were thus to (1) examine the effect of the live coral trade on the size/age frequency distributions of an exploited species *in situ* for the first time, (2) investigate the socio-economic characteristics of the trade and (3) explore the current and alternative harvesting regimes through an application of yield/utility per recruit analyses. A case study approach was taken in the Spermonde Archipelago (Fig.1), one of four major collections sites in Indonesia (Raymakers, 2001), and concentrated on the species with the region's highest trade quotas for the years 2004-2006, the mushroom coral *Heliofungia actiniformis* (BKSDA Makassar, 2006). Data on *H. actiniformis* population dynamics from natural, unfished populations was available for comparative purposes from a recent study (Knittweis, 2008).

Materials and Methods

Socio-economics

To assess the number of coral trading companies, licensed fishermen and the location of holding facilities in the Spermonde Archipelago, government records were requested from the

Makassar Natural Resources Conservation Agency (BKSDA, Balai Konservasi Sumber Daya Alam). During a subsequent semi-structured interview survey in June 2006, fishermen were asked about (1) *H. actiniformis* collection criteria (2) prices of individual polyps and (3) the location of *H. actiniformis* harvesting grounds.

Prices were converted to US$, using the exchange rate of the 15th June 2006 (1 US$ = 9478.673IDR). In addition, the length and colours of *H. actiniformis* polyps in holding tanks destined for sale were opportunistically recorded whenever possible. Three harvested sites (Kapodasang, Kudingareng Lompo and Bone Pute) as close as possible to the unharvested sites (Bone Baku, Samalona and Barrang Lompo) previously surveyed by Knittweis (2008) were selected based on survey results (Fig. 1).

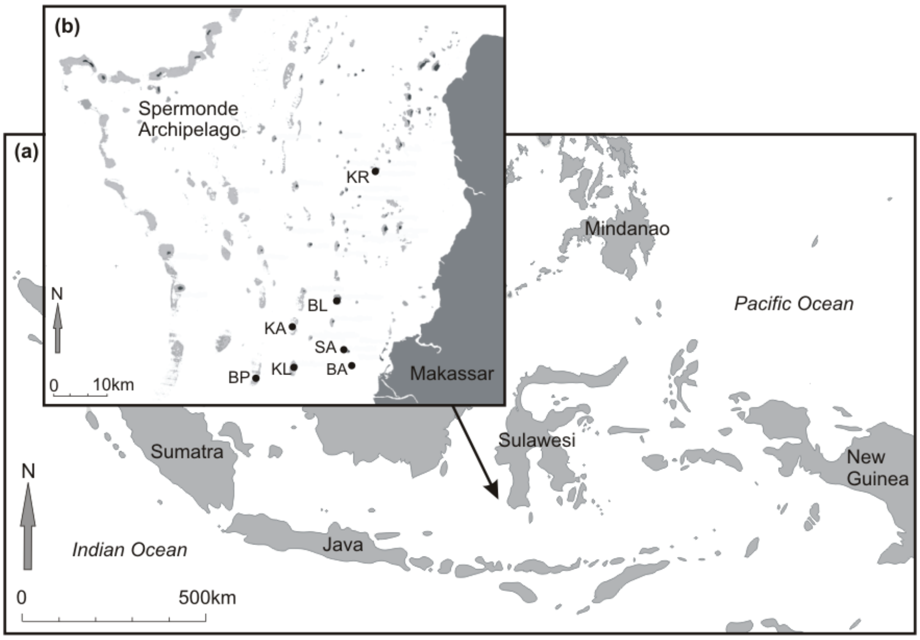

Fig. 1. (a) Location of Spermonde Archipelago within the Indo-Malay Archipelago (b) Sampling sites in the Spermonde Archipelago. BA: Bone Baku, SA: Samalona, BL: Barrang Lompo; KA: Kapodasang; KL: Kudingareng Lompo; BP: Bone Pute; KR: Karangrang (taken from Landsat ETM+ satellite image, acquisition year 2002).

Population structure and mortality rates

H. actiniformis population structure at harvested sites was surveyed by conducting belt transects parallel to the shore at 8, 12 and where applicable 16 m depth, thus covering the depth-range where *H. actiniformis* populations are concentrated (Knittweis, 2008). In order to ensure similarity of exposure and habitat type, all surveys were conducted on 150m by 6m belt transects on reef sides exposed to the north-western monsoon. Due to the clustered nature of *H. actiniformis* polyps, transects were only set after encountering a minimum of 5 polyps in a 3 m by 6 m area. Within each transect, all *H. actiniformis* polyps were examined and their length (along the mouth axis, after Abe, 1940), colour (whether commercially valuable or not) and life cycle stage recorded as (1) attached polyp on reef anthocaulus (2) attached polyp on adult skeleton or (3) detached, free-living polyp.

Density per 500m^2 was calculated to standardize estimates from unequal sampling areas, and size-frequency data was converted to age-frequency distributions based on the age-length relationship obtained by Knittweis (2008). Differences in population age structures between the harvested sites surveyed in this study and those known from unharvested sites were visualized through age histograms, and mean ages as well as the amount of variation in polyp ages (coefficient of variation, CV) of the distributions were calculated as proxies for the impact of harvesting on *H. actiniformis* populations.

Total mortality rates (Z) were calculated separately for the attached polyps (0-4 cm length), free-living polyps (4-11 cm length) currently being exploited by the aquarium trade and larger free living polyps (11-15 cm length) no longer targeted by fishermen. This was achieved by applying a length-converted catch curve analysis to the length-frequency data (Pauly, 1984) using von Bertalanffy growth parameters (k, L_∞) of *H. actiniformis* known for the Spermonde Archipelago (Knittweis, 2008). Individuals exceeding 15 cm in length were excluded from the analysis to eliminate inaccuracies in the relationship of length and age in larger polyps (Sparre and Venema, 1998). The significance of the differences between sample regression coefficients was tested by two-tailed student's t-tests, using a Bonferroni correction to adjust for the effects of multiple comparisons.

To describe the current state of the fishery, fishing mortality rates (F) were calculated by subtracting natural mortality rates (M) at unharvested sites (Knittweis, 2008) from total mortality rates (Z) at harvested sites. Exploitation rates (E) were subsequently obtained from F/Z (Gulland, 1971).

Current and potential economic yields

The current economic yield of the coral stock for each incoming recruit was determined by generating a Thompson & Bell yield table of the population based on available growth parameters and natural mortality rates (Knittweis, 2008), as well as the present values of fisheries mortality for each age group of the surveyed population. The potential yield was subsequently calculated with fishery mortality values below and above present levels, and after the hypothetical introduction of a 5 cm size limit, in order to explore the effect of these different potential fishery regimes on the profitability of the fishery.

Results

Socio-economics

At the time of surveying, 10 coral harvesting companies held licenses to operate within the Spermonde Archipelago: CV. Fadhil Utama, CV. Karang Mas, CV. Citra Samudra, UD. Usaha Coral, UD. Sukses Sejati, CV. Virly Jaya Abadi, CV. Dinar Cabang Makassar, CV. Rezky Bahari, CV. Rusdiana and CV. Umega. The average number of licensed fishermen per company was 5.6±2.9, with the trade's operational centers currently located on the islands Barrang Lompo and Karangrang (Fig. 1). Trade quotas for *H. actiniformis* in South Sulawesi (trade districts SulSel I and SulSel II), were stable at 6000 pieces from 1999-2002, rose by 1000 pieces to 7000 pieces in 2003 and stabilised at 9500 pieces in 2004-2006 (Fig. 2).

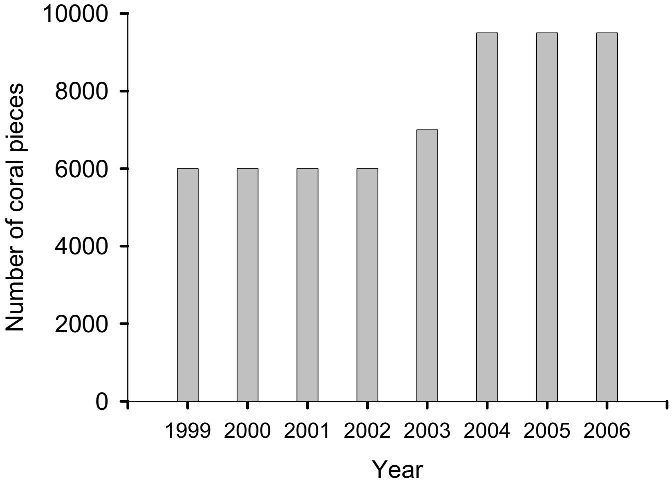

Fig. 2. *H. actiniformis* trade quotas for South Sulawesi (BKSDA Makassar, 2006).

Based on a total of 38 interviews with both licensed and unlicensed fishermen, as well as 4 middlemen, *H. actiniformis* prices were found to depend on polyp size and polyp colour (Table 1). Consumer demand was found to be for colourful small polyps that do not take up much space in home aquaria. Polyps of green body colour with white tentacle tips and brown/green body colour with purple tentacle tips sized 4-11cm are targeted by the fishermen, although the green body colour with white tentacle tips variety is far more common (Fig. 3).

Table 1 Mode of prices in US $ for *H. actiniformis* colour morphs.

	Polyp Size (cm)		
	3-5	**5-8**	**8-11**
Green Body	0.21 US$	0.42 US$	0.53 US$
Purple Tipped	0.32 US$	0.53 US$	0.74 US$

When young polyps are found to be still attached to the reef, common practice is to break off the entire cluster of small polyps (see Knittweis, 2008), keep only the largest polyps which have already developed a flat skeletal base, and discard the rest. Polyps larger than 11 cm are only rarely collected (Fig.3).

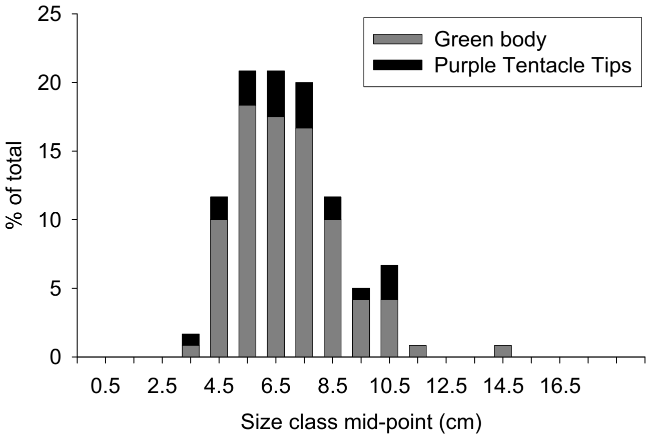

Fig. 3. Sizes/colour morphs of randomly surveyed *H. actiniformis* polyps harvested by fishermen in Barrang Lompo and Karangrang (n = 120).

H. actiniformis harvesting areas were located exclusively in the mid- and outershelf zones of the Spermonde Archipelago, where fishermen perceived potential police controls of harvest licenses to be less likely, and the more expensive colour morphs to be more abundant.

Population structure and mortality rates

The age frequency structure of *H. actiniformis* polyps showed populations dominated by young, attached individuals at harvested sites, with an average of 48±16% of polyps belonging to the 0-4 year age class interval. All attached polyps grew on stalks fixed to the reef, with an average of 2.7±2.8 polyps per cluster. Despite the much lower overall polyp abundances recorded at the harvested sites when compared to those reported from unharvested sites by Knittweis (2008) (Fig.4), the latter study also found 48% of polyps belonging to the 0-4 year age class, albeit with much lower variation.

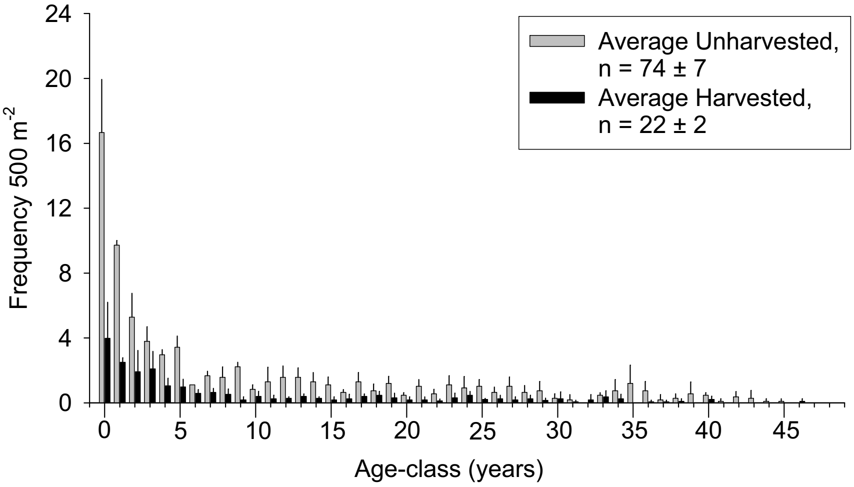

Fig. 4. Average age frequency structure of *H. actiniformis* polyps at harvested and unharvested sites in the Spermonde Archipelago, ± standard deviation.

Overall average ages at harvested and unharvested sites were similar, with 9.5±2.6 years and 10±2.3 years respectively. The coefficient of variation for the age-frequency distribution at the harvested sites was highest at Kapodasang (1.5), and lower at both Kudingareng Lompo (1.0) and Bone Pute (0.9). Except for a few exceptions at Kudingareng Lompo, polyps larger than 11 cm were all dull brown colour morphs of no commercial value.

Mortality rates at all three sites were highest for polyps sized 0-4 and 4-11 cm, and considerably lower for polyps sized 11-15 cm (Fig. 5). There were no significant differences between rates at the three surveyed sites (t value 0-4 cm: KA/KL = 0.93, KA/BP = 0.49, KL/BP = 1.15, t_{crit} = 3.94; t value 4-11 cm: KA/KL = 0.89, KA/BP = 1.50, KL/BP = 0.19, t_{crit} = 3.11; t value 11-15 cm: KA/KL = 1.68, KA/BP = 0.27, KL/BP = 1.25, t_{crit} = 3.94). Assuming initial larval recruitment to be the same as that previously found at unharvested sites (Knittweis, 2008), and substituting the catch curve plot of the harvested site with the average recruit number found in the unharvested site (Fig. 5), differences in total mortality rates (Z) for polyps at harvested compared to unharvested sites were significant for both the attached 0-4 cm size class (t = 3.17, t_{crit} = 3.94) and the small detached polyps sized 4-11 cm (t = 3.23, t_{crit} = 3.11), but not for the larger detached polyps measuring 11-15 cm in length (t = 0.63, t_{crit} = 3.94).

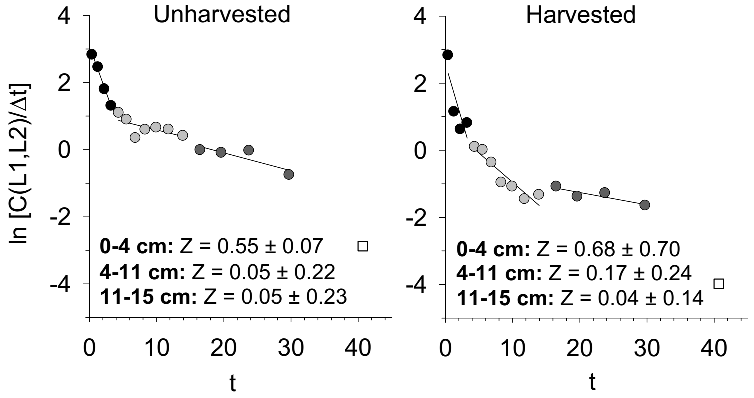

Fig. 5. Linearized catch curves based on length composition data for *H. actiniformis*. 0-4 cm: black circles (unharvested: $r^2 = 0.99$, $p = 0.004$/harvested: $r^2 = 0.68$, $p = 0.175$); 4-11 cm: light grey circles (unharvested: $r^2 = 0.42$, $p = 0.113$/harvested: $r^2 = 0.88$, $p = 0.002$); 11-15 cm: dark grey circles (unharvested: $r^2 = 0.73$, $p = 0.15$/harvested: $r^2 = 0.78$, $p = 0.12$); 16 cm: white square.

Fishing mortality rates were similar for polyps in the 0-4 cm and 4-11 cm size classes, with F = 0.127 and 0.124 respectively. As a result of the differences in total (Z) and natural mortality rates (M) in the two size class intervals, exploitation rates however were far lower for polyps measuring 0-4 cm in length than for those in the 4-11 cm size class, with E = 0.1 and 0.7 respectively.

Current and potential economic yields

Economic yield per recruit peaked at an age of 5 years and a size of ~5 cm, with 0.042 US$ per recruit (Table 2). This is 5 years before the estimated age of reproductive maturity (Abe, 1940) and 15 years before reaching the point where losses due to natural mortality start overtaking biomass gains due to growth (Knittweis, 2008).

The results of the application of the Thompson and Bell model (Fig. 6) show that relative to current fishing efforts, decreasing fishing mortality in the Spermonde Archipelago by 20% would entail only a minor reduction of the profit margin from 16.8 US$/1000 recruits to 16.7$/1000 recruits. Concurrently the number of polyps removed would be lowered from 215 per 1000 recruits to 184 per 1000 recruits. However, a decrease in fishing mortality rates by 60% would be needed to lower exploitation rates for polyps sized 4-11 cm to a point where fishing mortalities do not exceed natural mortalities, and E = 0.5.

Table 2 Age, size, survival and biomass/economic yields of the mushroom coral *H. actiniformis* in the Spermonde Archipelago, Indonesia. Calculations are for a hypothetical situation, with all recruits assumed to be green body colour/white tentacle tips colour morphs.

Age (yrs)	Length (cm)	Skeletal Mass (g)	Survival	Biomass Yield (g recruit-^{1})	Economic Yield (US$ cent recruit^{-1})
0	0.00	0.0	1.000	0.00	0.00
1	1.17	0.2	0.571	0.092	0.00
2	2.25	1.1	0.326	0.360	0.00
3	3.25	3.3	0.186	0.606	0.00
4	4.19	6.9	0.106	0.730	2.24
5*	**5.05**	**11.9**	**0.099**	**1.184**	**4.19**
6	5.86	18.5	0.093	1.718	3.93
7	6.60	26.2	0.087	2.283	3.68
8	7.29	35.1	0.082	2.865	3.45
9	7.93	44.9	0.076	3.437	3.23
10**	**8.54**	**55.9**	**0.072**	**4.004**	**3.78**
11	9.09	67.1	0.067	4.506	3.54
12	9.60	78.8	0.063	4.956	3.32
13	10.09	91.3	0.059	5.375	3.11
14	10.53	103.5	0.055	5.708	2.91
15	10.94	115.8	0.052	5.983	2.73
16	11.33	128.4	0.048	6.212	2.55
17	11.68	140.4	0.045	6.364	2.39
18	12.01	152.4	0.042	6.470	2.24
19	12.32	164.2	0.040	6.532	2.10
20***	**12.60**	**175.4**	**0.037**	**6.537**	**1.97**
21	12.87	186.7	0.035	6.517	1.84
22	13.11	197.2	0.033	6.445	1.72
23	13.34	207.5	0.031	6.354	1.62
24	13.55	217.3	0.029	6.232	1.51
25	13.75	226.9	0.027	6.095	1.42
26	13.93	235.7	0.025	5.931	1.33
27	14.10	244.3	0.024	5.758	0.00
28	14.26	252.5	0.022	5.575	0.00
29	14.41	260.4	0.021	5.386	0.00
30	14.54	267.4	0.019	5.180	0.00

* Maximum economic yield

** Age of reproductive maturity (Abe, 1937)

*** Maximum biomass production

Testing the introduction of a 5 cm minimum collection size limit showed the potential for considerably increased profits at a much lower number of *H. actiniformis* polyps harvested. If fishing efforts remained constant and only detached polyps ≥5 cm were to be collected, profits could actually rise from ~17 US$ per 1000 recruits to ~29 US$ per 1000 recruits, with a much lower total number of polyps collected.

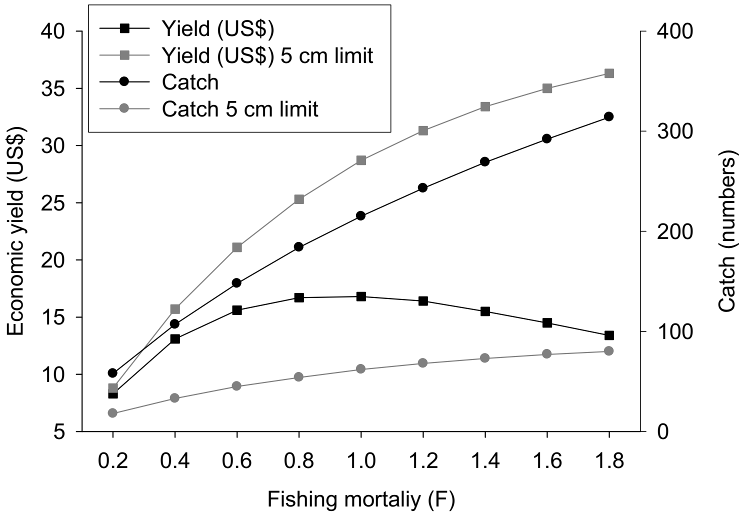

Fig. 6. Catch/value of *H. actiniformis* fishery at different fishing mortality rates relative to the current situation in the Spermonde Archipelago (F = 1). Thompson and Bell model calculations are per 1000 polyps, assuming constant recruitment rates; prices are for polyps with green body colour.

Discussion

The questionnaire on *H. actiniformis* fishing practices revealed very distinct collection criteria driven by consumer demand, with brightly coloured polyps small enough to fit into home aquaria as the main target of fishermen in Spermonde. The estimates of coral prices were surprisingly low, with fishermen only receiving about 30-70 US$ cents (depending on size) for the most expensive colour morphs, which consumers in Europe and the US purchase for the tenfold amount (Knittweis, personal observation). Although a few companies directly employ fishermen who go on 2-3 day trips and exclusively collect corals, using company boats and equipment, more frequently groups of family members make up fishing parties, which collect everything from fish for subsistence use, sea cucumbers, larger fish for sale as well as coral and ornamental fish. Upon their return fishermen bring the collected coral to middlemen, who fix prices and frequently discard considerable proportions of the catch, as evidenced by piles of ornamental coral skeletons outside the majority of holding facilities.

The surveys also revealed an unfortunate practice regarding the harvest of small polyps. Young *H. actiniformis* grow attached to the substratum by a stalk before detaching, usually at a size of 3- 4cm, although attached polyps up to 7 cm have been observed (Knittweis, 2008). Fishermen mainly begin targeting polyps when they reach a size of ~4 cm (Fig. 3), but the two smallest polyps observed for sale in this study measured 3 and 3.8 cm. Both had visible recent detachment scars, as did a number of polyps in the 4-5 cm size class. During related interviews fishermen stated that clusters of attached polyps are routinely harvested and that only the largest polyps which have developed a flat base are kept, whilst the rest is discarded on site. Whenever a cluster has grown in a nice shape, it is kept intact and sold to middlemen as *Euphyllia glabrescens*. Due to the similarity of the tentacles and early growth morphology of *H. actiniformis* it is difficult to tell the two species apart. Indeed, when shown pictures of *H. actiniformis* anthocauli and small colonies of *E. glabrescens*, none of the fishermen or middlemen interviewed could distinguish between the two species.

A higher number of *H. actiniformis* than allowed by current quotas is thus being harvested if (1) discarded by-catch and (2) attached polyps sold as *Euphyllia* sp. are taken into account. The reluctance of some fishermen to be interviewed, the fact that many of the fishermen did not have licenses and admitted avoiding police controls, and the experience that it was impossible to gain access to holding tanks in order to monitor polyp landings further point towards the limits of current trade management attempts. Illegal exportation of corals without permits from Makassar was already described in 1998 (Bentley, 1998).

The most critical assumption made when comparing control and impact sites is that the parameter of interest (i.e. *H. actiniformis* population demographics) is similar at both sites prior to the onset of the impact (i.e. harvesting) (Osenberg and Schmitt, 1996). Hoeksema surveyed mushroom coral populations in the Spermonde Archipelago in 1989 and indeed found *H. actiniformis* to have similar abundances at Samlona and Kapodasang (Hoeksema, 1989), which today are markedly different due to harvesting activities at Kapodasang. Whilst repeated surveying of size-frequency is recommended in population demographic assessments to take into account recruitment events (Pauly, 1984), Knittweis (2008) found no correlation between the strength of 0-4 cm size classes and sampling season over a two year period, so that a single population census indeed seems to give an accurate representation of population structure in *H. actiniformis* during the study period.

Comparing *H. actiniformis* population structures surveyed at harvested sites over the course of this study and those known from unharvested sites (Knittweis, 2008) revealed (1) a marked decline in the overall abundance of polyps at harvested sites, particularly in young, attached polyps (Fig. 4) and (2) significantly higher total mortality rates for polyps in the 0-4 and 4-11 cm size classes. Based on the results of the questionnaire surveys this lower abundance of young *H. actiniformis* polyps found at harvested sites was assumed to be entirely due to direct effects of harvesting, as opposed to stock-recruitment effects. This assumption is validated by the fact that Knittweis et al. (2008) found panmixia of *H. actiniformis* larvae between nearshore sites. Abe (1937) estimated the swimming period of *H. actiniformis* larvae at 2-3 days, which would give sufficient time for dispersal, especially if larvae are caught in currents.

Decreases in the average age of harvested populations have in the past been recorded for *Pocillopora verrucosa* in the Philippines (Ross, 1984), the black corals *Anthipates dichotoma* and *Anthipates grandis* (Grigg, 2001) as well as the red coral *Corallium rubrum* (Tsounis et al. 2007), with decreases being a result of the demand for large coral colonies by the trade. In the present study, a different situation was found with fishermen targeting small polyps, a pattern suggested by the results of the socio-economic survey as well as the age-frequency distributions, and confirmed by the statistical difference in mortality rates for polyps aged 0-11 years when compared to those of natural populations (Fig. 5).

The exploitation (E) rates calculated showed that whilst polyps sized 0-11 cm are being targeted by the fishery, the main fishing pressure is on corals measuring 4-11 cm in length, where E = 0.7. Gulland proposed that a fishery is approximately at an optimal level when natural mortality rates equal fishing mortality rates (i.e. E = 0.5) (Gulland, 1971), and this expression has been widely used in determining the potential yields of fish stocks. With E = 0.7 *H. actiniformis* polyps in the 4-11 cm size class are thus clearly suffering from overexploitaton in the Spermonde Archipelago. Moreover, subsequent work by a number of authors showed E = 0.5 to be a rather risky exploitation strategy, and suggested that even lower E values should be considered for a fishery to be sustainable (Beddington and Cooke, 1983; Patterson, 1992).

Maximum biomass yield per recruit has been estimated to occur at a polyp age of 20 years and a related length of ~12-13 cm in *H. actiniformis* (Knittweis, 2008). When put into perspective based on the results obtained by this study, it however becomes clear that maximum biomass yield peaks at a point when all but a few exceptionally brightly coloured polyps are worthless to fishermen due to their large size. The utility per recruit paradigm is thus more suited to the development of potential harvest management recommendations in this fishery. Maximum economic yield per recruit occurs at an age of 5 years and a corresponding size of ~5 cm in *H. actiniformis* (Table 2), with a value of 4.19 US$ cents per recruit. Growth/economic overfishing is thus taking place at the moment: despite the much lower prices being paid by middlemen for polyps smaller than 5 cm (Table 1) these are being harvested in considerable numbers.

An application of the Thompson and Bell model revealed that the introduction of a 5 cm size limit could potentially increase profits by 58% (Fig. 6). This underlines the severity of current growth overfishing, exacerbated by the current practice of discarding a significant proportion of small, attached polyps. The markedly lower average number of young polyps per cluster found in the present study (n = 2.7±2.8) when compared to unharvested sites (n = 5.4±4.5) further indicates that settled larvae are not given a chance to produce the stalk clusters naturally present in *H. actiniformis* (Knittweis, 2008). Setting such a size limit in order to maximize yields would thus have the added benefit of protecting anthocaulus stalks, and thus allow for a constant release of asexually produced *H. actiniformis* polyps into the system.

Moreover, in order to achieve long term sustainability, exploitation rates for polyps in all size class should at the very least never exceed E = 0.5. According to the Thompson and Bell calculations, a 60% decrease of fishing mortality rates for polyps sized 4-11 cm relative to the current situation would be needed to achieve this. In combination with the introduction of a 5 cm size limit, this could in fact be achieved without lowering profits (Fig. 6).

In addition to growth/economic overfishing, the issue of recruitment overfishing also needs to be taken into consideration. Although mature polyps from nearby unharvested nearshore sites will have an input of larvae at the studied sites, this will not be the case for harvested sites in the midshelf regions of the archipelago, where a similarly limited number of reproductively mature polyps aged 10 years or more would in the long term preclude a sufficient input of larvae to the system.

Furthermore, virtually all detached polyps remaining at the three sites surveyed were found to be of dull, brown body colour with white tentacle tips, which have no commercial value. Whilst such polyps will safeguard *H. actiniformis* from being harvested to extinction as a species, their larval input into the system may not necessarily help to ensure long term trade sustainability. Coral colour arises from two sources: the presence of symbiotic zooxanthellae, which impart a brown colour of variable intensity depending on light conditions (e.g. Hoegh-Guldberg and Smith, 1989), as well as pigments associated directly with coral tissues (Kawaguti, 1944), which seem to be responsible for the sometimes brilliant green, red and blue reef colours. Whilst very little is known about the heredity of coral colour to date, Takabayashi and Hoegh-Guldberg (1995) showed that although the extent of pigment expression was influenced by environmental factors, genetic differences did determine the differences between two colour morphs of *Pocillopora damicornis*. It is thus likely that whilst there may be a hidden nearshore genetic reservoir of bright *H. actiniformis* colour morphs lacking phenotypic expression as a result of the more turbid waters, the marked reduction of large colourful polyps capable of emitting substantial numbers of similar larvae in the archipelago as a whole is in fact rendering the dangers of recruitment overfishing even more severe than one may conclude by looking at Fig. 4 alone.

In order to protect spawning stocks and curb the problem of recruitment overfishing, a stricter enforcement of existing marine protected areas throughout the Spermonde Archipelago in combination with quota reductions should thus be made priorities. At the very least the recent harvest quota increases, made without sufficient scientific basis (Fig. 2) should be revoked based on the results of this investigation. Unfortunately, as was observed when carrying out the socio-economic surveys, the small, traditional and personalized networks of the industry provide many routes of illegal harvesting. Enforcement of existing legislation to protect marine resources in general is poor in the region (Knittweis, personal observations), as are levels of awareness and education, illustrated in this case by the high levels of by-catch and inability of traders to distinguish between young *H. actiniformis* and *E. glabrescens*. Clearly, more resources need to be devoted to solving such problems if any management regimes are to actually be implemented rather than simply existing on paper as is frequently the case today.

Conclusion

The long term sustainability in the *H. actiniformis* fishery can thus only be achieved by a combination of (1) introducing a 5 cm harvest size limit (2) lowering current fishing mortalities by at least 60% (3) protecting spawning stocks (4) generally improving levels of awareness and law enforcement. In addition, investigations similar to the current study are urgently needed for the many remaining species of ornamental coral being harvested in Spermonde if the region’s live coral aquarium trade as a whole is to achieve long term sustainability.

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References

Abe, N., 1937. Post-larval development of the coral *Fungia actiniformis* var. palawensis Doederlein. Palau Trop. Biol. Station Stud. 1, 73-93.

Abe, N., 1940. Growth of *Fungia actiniformis* var. palawensis Doederlein and its environmental conditions. Palao Trop. Biol. Station Stud. 2, 105–145.

Bak, R.P.M., Meesters E.H., 1999. Population structure as a response of coral communities to global change. Amer. Zool. 39, 56-65.

Beddington, J.R., Cooke, J.G., 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 pp.

Bentley, N., 1998. An overview of the exploitation, trade and management of corals in Indonesia. Traffic Bull.17, 67–78.

Beverton, R.J.H., Holt, S.V., 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food Ser. II 19, 1-553.

Brown, B.E., Clarke K.R., 2002. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to effects of local (sedimentation) and regional (climatic) perturbations. Mar. Biol. 141: 21-29.

Bruckner, A.W., 2002. Proceedings of the international workshop on the trade in stony corals: development of sustainable management guidelines. NOAA Technical Memorandum NMFS-OPR-23, Silver Spring, MD, 152 pp.

Chadwick-Furman, N.E., Goffredo, S., Loya, Y., 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. J. Exp. Mar. Biol. Ecol. 254, 199-218.

Die, D.J., Restrepo, V.R., Hoenig J.M., 1988. Utility-per-recruit modelling: a neglected concept. T. Am. Fish. Soc. 117, 274-281.

Done, T.J., 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus Porites: evidence of population resilience? Coral Reefs 6, 75-90.

Gilmour, J.P., 2004. Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. Coral Reefs 23, 494-504.

Goffredo, S., Chadwick-Furman, N.E., 2003. Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea. Mar. Biol. 142, 411-418.

Goffredo, S., Mattioli, G., Zaccanti, F., 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Coral Reefs 23, 433-443.

Green, E.P, Shirley, F., 1999. The global trade in corals. World Conservation Monitoring Centre. World Conservation Press, Cambridge UK, 60 pp.

Grigg, RW., 1976. Fisheries management of precious and stony corals in Hawaii. UNIHI Sea Grant Tr. 77/03, 1-48.

Grigg, R.W., 1984. Resource management of precious corals: a review and application to shallow water reef building corals. P.S.Z.N.I. Mar. Ecol. 5, 57–74.

Grigg, R.W., 2001. Black coral: history of a sustainable fishery in Hawaii. Pac. Sci. 55, 291-299.

Groeneveld, J.C., 2000. Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. Fish. Res. 48, 141-155.

Gulland, J.A., 1971. The fish resources of the oceans. West fleet survey. Fishing News Ltd., FAO, 255pp.

Hoegh-Guldberg, O., Smith, G.J., 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. J. Exp. Mar. Biol. Ecol. 129, 279-303.

Hoeksema, B.W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zool. Verhand. 254, 1-295.

Hughes, T.P., 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70, 275-279.

Hughes, T.P., Jackson, J.B.C., 1980. Do Corals Lie About Their Age? Some Demographic Consequences of Partial Mortality, Fission, and Fusion. Science 209, 713-715.

Jones, R., 2008. CITES, corals and customs: a review of the international trade in wild coral. In: Proceedings of the 1st International Coral Husbandry Symposium, Arnhem, Holland, in press.

Kawaguti, S., 1944. On the physiology of reef corals. Study on the pigments. Palao Trop. Biol. Station Stud. 2, 617-673.

Kirchner, C.H., 2001. Fisheries regulations based on yield-per-recruit analysis for the linefish silver kob *Argyrosomus indodorus* in Namibian waters. Fish. Res. 52, 155-167.

Knittweis, L., 2008. Population Demographics and Life History Characteristics of *Heliofungia actiniformis*, a Fungiid Coral Species Exploited for the Live Coral Aquarium Trade in the Spermonde Archipelago, Indonesia. Ph.D. thesis, University of Bremen.

Knittweis L., Kraemer W.E., Timm J., Kochzius M., 2008. Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. Conserv. Genet., doi: 10.1007/s10592-008-9566-5.

Meesters, E.H., Hilterman M., Kardinaal, E., Keetman, M., de Vries M., Bak, R.P.M., 2001. Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar. Ecol. Prog. Ser. 209, 43-54.

Nevarez-Martinez, M.O., Mendez-Tenorio F.J., Cervantes-Valle C., Lopez-Martinez J., Anguiano-Carrasco M.L., 2006. Growth, mortality, recruitment and yield of the jumbo squid (*Dosidicus gigas*) off Guayamas, Mexico. Fish. Res. 79, 38-47.

Osenberg, C.W., Schmitt, R.J., 1996. Detecting ecological impacts caused by human activities. In: Detecting ecological impacts: concepts and applications in coastal habitats. Academic press, San Diego, California, pp. 3-16.

Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. Re. Fish. Biol. Fisher. 2, 321-338.

Pauly, D., 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Stud. Rev. 8. 325pp.

Ross, M.A., 1984. A quantitative study of the stony fishery in Cebu, Philippines. Mar. Ecol. Pubbl. Stn. Zool. Napoli 5, 75-91.

Raymakers, C., 2001. Review of trade in live corals from Indonesia. Traffic Europe, Brussels, 18 pp.

Sparre, P., Venema, S.C., 1998. Introduction to tropical fish stock assessment. FAO Fisheries Technical Paper 306/1. 407pp.

Takabayashi, M., Hoegh-Guldberg, O., 1995. Ecological and physiological differences between two colour morphs of the coral *Pocillopora damicornis*. Mar. Biol. 123, 705-714.

Thompson, W.F., Bell F.H., 1934. Biological statistics of the Pacific halibut fishery. 2. Effect of changes in intensity upon total yield and yield per unit of gear. Rep. Int. Fish. Comm. 8, 49pp.

Tsounis, G., Rossi, S., Gili, J.M., Arntz, W., 2006. Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). Mar. Biol. 149, 1059-1070.

Tsounis G., Rossi S., Gili J.M., Arntz W., 2007. Red coral fishery at the Costa Brava (NW Mediterranean): case study of an overharvested precious coral. Ecosystems 10, 975-986.

Vermeij, M.J.A., Bak, R.P.M., 2002. Inferring demographic processes from population size structure in corals. In: Proceedings of the 9th International Coral Reef Symposium, Vol. 1, 589-593.

von Bertalanffy L., 1928. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10, 181-213.

Wabnitz, C., Taylor, M., Green E., Razak, T., 2003. From ocean to aquarium. UNEP-WCMC, Cambridge, UK, 66 pp.

Appendix

Disclaimer

Traditional Indonesian fishing boat

Gemäß §6 der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007 versichere ich, dass:

1. die Arbeit ohne unerlaubte fremde Hilfe angefertigt wurde
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3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht wurden

Bremen, 10. April 2008

(L. Knittweis)